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BREVIORA

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NUMBERS 121-178

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Museum of Comparative Zoology

CAMBRIDGE, MASS. MARCH 10, 1960 NUMBER 121

THREE NEW SPECIES OF MICRATHENA (ARANEAE, ARGIOPIDAE) FROM SOUTH AMERICA

By ARTHUR M. CHICKERING

Albion College, Albion, Michigan

During the summer of 1959 I had the privilege of examining the South American Micrathenae in the Museum of Comparative Zoology at Harvard College. Among the specimens in this collection I found representatives of what I am compelled to regard as new species. I am describing these in this brief paper under the names: *Micrathena hamata* sp. nov.; *M. lata* sp. nov.; and *M. shealsi* sp. nov. I have also added a few notes together with figures illustrating features of the epigynum of *M. fissispina* (C. L. Koch), 1836, with the hope that they will aid somewhat in a more precise identification of this species. The types of the new species are deposited in the Museum of Comparative Zoology.

It is with pleasure and a deep sense of gratitude that I again acknowledge my indebtedness to members of the staff of the Museum of Comparative Zoology at Harvard College for their continued encouragement over a period of more than twenty-five years. Persons now active on the staff of the museum and chiefly responsible for this encouragement may be specifically named as follows: Dr. A. S. Romer, Director; Dr. P. J. Darlington, Jr., Curator of Insects; Dr. Herbert W. Levi, Associate Curator of Arachnology; Miss Nelda E. Wright, Editor of Publications. Several other members of the museum staff have also greatly aided me by providing privileges of the laboratories, collections, and library.

Micrathena fissispina (C. L. Koch), 1836
(Figures 1-3)

Acrosoma fissispina C. L. Koch, 1836

Plectana fissispina Walckenaer, 1841

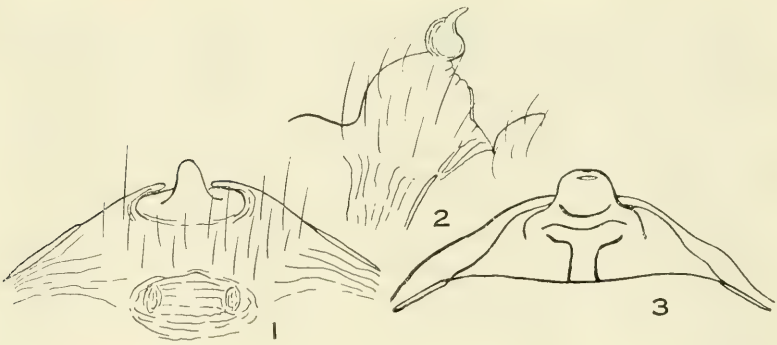
M. fissispina Simon, 1895

M. fissispina Reimoser, 1917

M. fissispina Roewer, 1942

M. fissispina Bonnet, 1957

There are three mature females in the Nathan Banks Collection in the Museum of Comparative Zoology. These are simply labelled as having come from Brazil with no dates of collection



External Anatomy of *Micrathena*

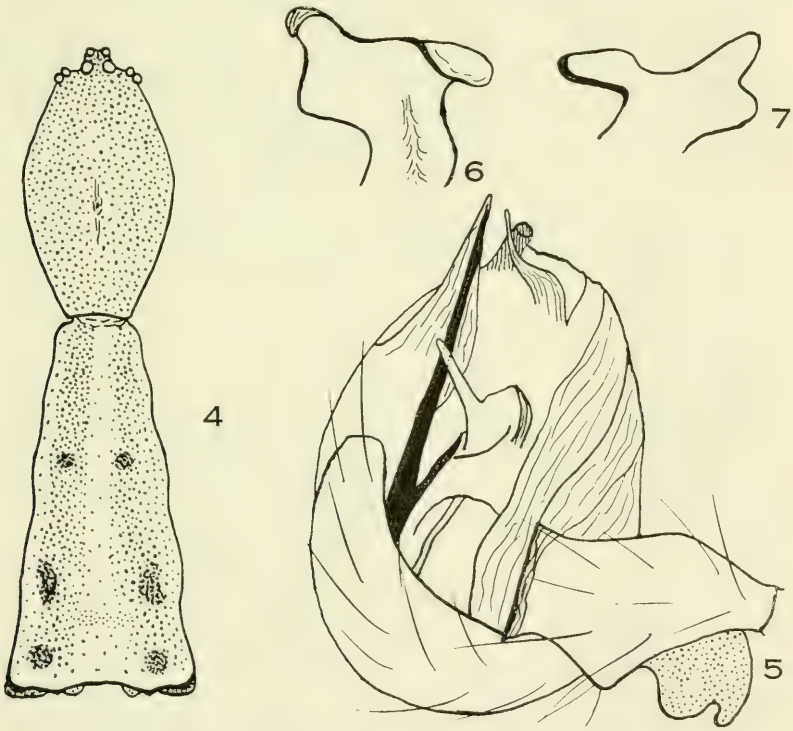
Figures 1-3. *M. fissispina* (C. L. Koch).

Figs. 1-3. Epigynum: from below; profile, right side; posterior surface, respectively.

assigned. The abdominal spination is a fairly reliable feature for identification, but the epigynum is also important. Since this organ appears somewhat different than represented in Reimoser's (1917) figures I am offering three more drawings with the hope that they will help others to a more exact identification of this species. The male remains unknown.

Micrathena hamata sp. nov.
(Figures 4-7)

The two mature males treated in this part of this paper were found filed in the Banks Collection in the Museum of Comparative Zoology with females considered to belong to *M. petersi* (Tacz.). The females are probably immature specimens of *M. sexspinosa* (Hahn). The males appear to be new to science and, consequently, one has been selected as the holotype and is herewith described in accord with my usual procedure.



External Anatomy of *Micrathena*
Figures 4-7. *M. hamata* sp. nov.

Fig. 4. Body of male, dorsal view.
Fig. 5. Left palpal tarsus and tibia.
Fig. 6. Palpal tarsal hook; nearly retrolateral view.
Fig. 7. *Ibid.*, a different view.

Male holotype. Total length 4.68 mm. Carapace 1.92 mm. long, 1.105 mm. wide opposite second coxae where it is widest; .455 mm. tall; nearly level from behind PME to beginning of posterior declivity. Median thoracic fovea a shallow longitudinal depression. Dorso-lateral foveae lacking.

Eyes. Eight in two rows as usual in the genus; lateral ocular tubercles weakly developed; median ocular tubercles bearing ME quite pronounced. Viewed from above, both rows strongly recurved; viewed from in front, anterior row nearly straight, posterior row moderately procurved; central ocular quadrangle wider behind than in front in ratio of 22 : 17, about as long as wide behind. Ratio of eyes AME : ALE : PME : PLE = 6 : 6.5 : 8 : 5.5 (long diameter used when there are differences). AME separated from one another by four-thirds of their diameter, from ALE by nearly five-halves of their diameter. PME separated from one another by nearly three-halves of their diameter, from PLE by about three-halves of their diameter. Laterals separated from one another by two-thirds the diameter of AME. Clypeus strongly receding; height equal to about twice the diameter of AME.

Chelicerae, Maxillae, and *Lip.* Apparently quite normal for males in the genus. Fragility of specimen precludes examination of fang groove for marginal teeth.

Sternum. Very rugulose; with a marked transverse groove between third and fourth coxae; fourth coxae nearly touching.

Legs. 4123. Width of first patella at "knee" .11913 mm., tibial index of first leg 11. Width of fourth patella at "knee" .12996 mm., tibial index of fourth leg 13.

(All measurements in millimeters)

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
1.	.990	.374	.748	.594	.418	3.124
2.	1.012	.396	.660	.550	.396	3.014
3.	.704	.264	.396	.330	.352	2.046
4.	1.078	.330	.706	.660	[1].450	3.224
Palp	.400	.220	.330	——	[2].682	1.632

[1] Estimated because of loss of both fourth tarsi.

[2] Including tarsal hook.

There is no ventral hook on first coxa nor any corresponding proximal, prolateral femoral ridge and groove on the second femur. There also seems to be a complete lack of modified spines on the legs.

Palp. Essential features shown in Figures 5-7. The tarsal hook and tibia appear to be quite distinctive.

Abdomen. General shape as shown in Figure 4. It seems highly probable that the female of the species will be found to have a series of prominent paired spines, remains of which seem to be present in the male.

Color in alcohol. Carapace a nearly uniform rich reddish brown. Sternum somewhat lighter. Legs and mouth parts with various shades of brown. Abdomen: Dorsum yellowish along each dorso-lateral margin; broadly and irregularly brownish in the middle with a central lighter irregular stripe and some indication of reduced black spots; venter irregularly brownish, yellowish and nearly black.

Type locality. Holotype male and one paratype male in the Nathan Banks Collection from Para, Brazil. No date of collection is given. The female is unknown.

Micrathena lata sp. nov.
(Figures 8-12)

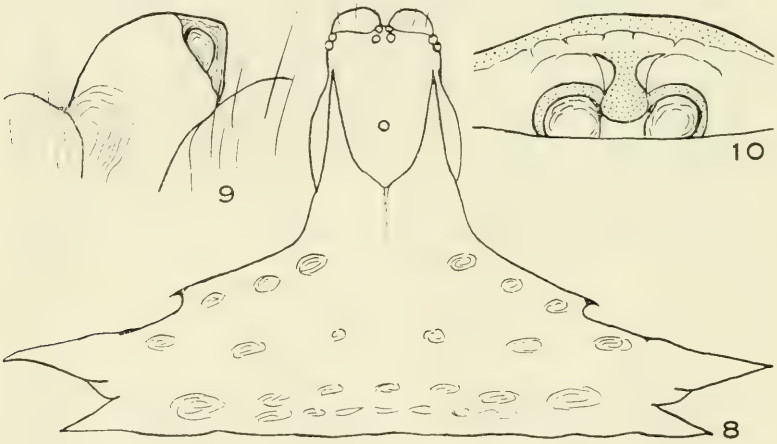
The specimen described below was filed in the Reimoser Collection in the Museum of Comparative Zoology at Harvard College as *M. digitata* (C. L. Koch). This is obviously an error and, since I can find no record of it in the literature I am compelled to regard it as new and am describing it as such.

Female holotype. Total length from anterior margin of base of chelicerae to posterior border of abdomen 7.15 mm. Width of abdomen at base of anterior spines 2.925 mm.; width between tips of larger posterior spines 13.325 mm. Carapace smooth; with median thoracic fovea a well defined pit; not markedly raised behind median fovea; with no dorso-lateral foveae.

Eyes. Eight in two rows as usual in the genus. Viewed from above, both rows moderately recurved; viewed from in front, anterior row nearly straight, posterior row gently procurved. Central ocular quadrangle wider behind than in front in ratio of about 3 : 2; wider behind than long in ratio of 9 : 7. Ratio

of eyes AME : ALE : PME : PLE = 8 : 8 : 10 : 8.5. AME separated from one another by five-fourths of their diameter, from ALE by six times their diameter. PME separated from one another by three-halves of their diameter, from PLE by nearly six times their diameter. Laterals separated from one another by three-eighths of the diameter of ALE. Height of clypeus equal to about seven-fourths of the diameter of AME.

Chelicerae. Normal to genus; unable to observe teeth along fang groove because of fragility of holotype.



External Anatomy of *Micrathena*
Figures 8-10, *M. lata* sp. nov.

Fig. 8. Outline of body of female holotype; dorsal view.

Figs. 9, 10. Epigynum; profile, right side and posterior surface, respectively.

Lip and *Maxillae.* Normal to genus; details considered unimportant in the description.

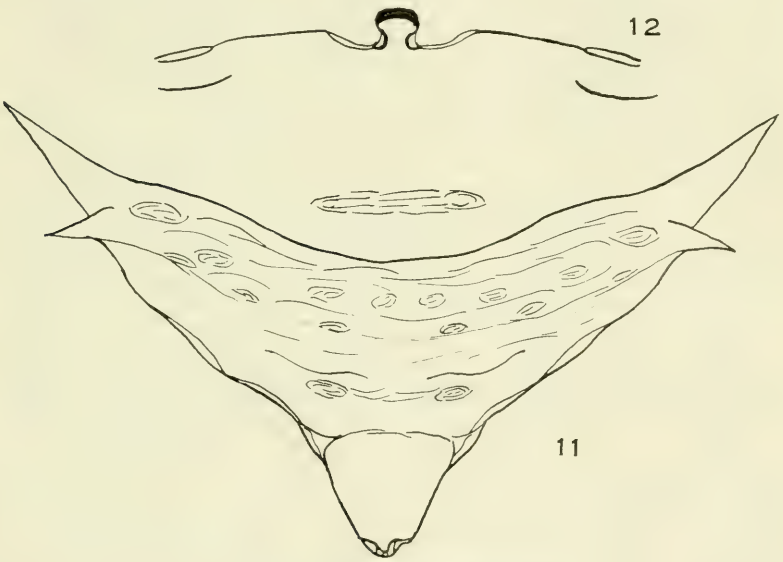
Sternum. Extended; with deep lateral notches and with six exaggerated marginal tubercles; with posterior end extended between fourth coxae as a prominent tubercle nearly one-third as long as entire sternum.

Legs and *Spines.* Only two legs remain entire, hence details not recorded. In general quite normal to genus. True spines

rare; the usual numerous setigerous tubercles moderately well developed.

Abdomen. Extraordinarily broadened posteriorly; with a pair of nearly straight anterior marginal spines extended nearly to PME; with a pair of very small lateral marginal spines; the posterior end is broadly bifurcated and each fork is subdivided into two spines thus making a total of eight.

Epigynum. General features shown in Figures 9, 10, and 12.



External Anatomy of *Micrathena*
Figures 11 and 12, *M. lata* sp. nov.

Fig. 11. Posterior end of female holotype.
Fig. 12. Epigynum, from below.

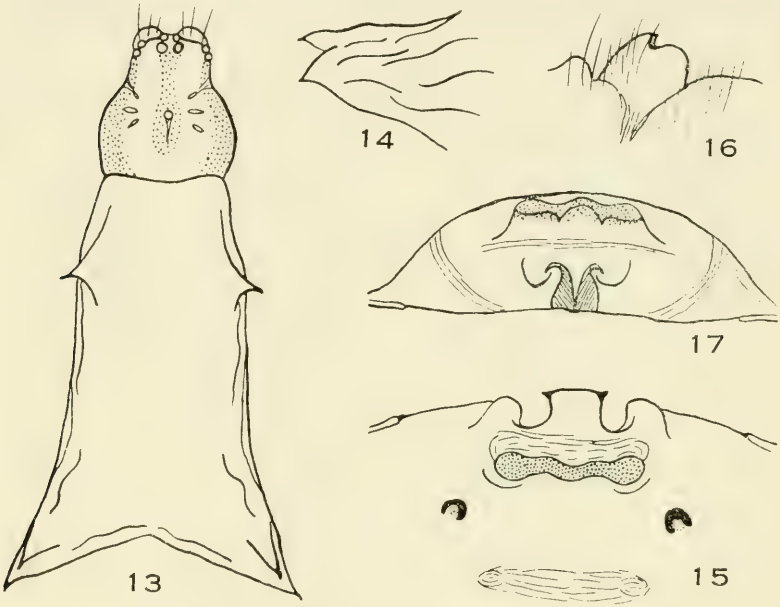
Color in alcohol. Light reddish brown with dark streaks and irregular spots.

Type locality. Holotype female from Theresapolis, Brazil, with no date of collection given. There are no paratypes and the male is unknown.

MICRATHENA SHEALSI sp. nov.

(Figures 13-17)

Female holotype. Total length from AME to tip of posterior spines 9.23 mm. Carapace 2.79 mm. long; 2.08 mm. wide opposite second coxae where it is widest; about .98 mm. tall behind well



External Anatomy of *Micrathena*

Figures 13-17, *M. shealsi* sp. nov.

Fig. 13. Outline of female holotype, dorsal view.

Fig. 14. Right lateral side of abdomen to show spines on bifurcation.

Figs. 15-17. Epigynum: from below, right lateral side, and from posterior view, respectively.

defined median fovea where it is strongly gibbous; with three pairs of dorso-lateral foveae as represented in Figure 13.

Eyes. Eight in two rows as usual; viewed from above, both rows moderately recurved; viewed from in front, both rows

gently procurved, measured by centers. Central ocular quadrangle wider behind than in front in ratio of about 8 : 7, only slightly wider behind than long. AME separated from one another by their diameter, from ALE by nearly 3.5 times their diameter. PME separated from one another by their diameter, from PLE by three times their diameter. Ratio of eyes AME : ALE : PME : PLE = 10 : 10 : 12 : 7 (long diameters used when differences exist). Laterals separated from one another by nearly the radius of ALE. Height of clypeus equal to nearly 1.2 times the diameter of AME.

Chelicerae. In general, normal to the genus; promargin of fang groove with three teeth, the middle one bidental; retromargin with three large teeth.

Maxillae. Apparently completely typical of the genus in all observed features.

Lip. Wider than long in ratio of about 4 : 3; transversely grooved in basal third. Sternal suture procurved.

Sternum. Elongated scutiform; moderately convex; only with well developed antero-lateral tubercles; not continued between fourth coxae; sparsely supplied with moderately long stiff bristles.

Legs. 4123. Width of first patella at "knee" .325 mm., tibial index of first leg 11. Width of fourth patella at "knee" .303 mm., tibial index of fourth leg 11.

(All measurements in millimeters)

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
1.	2.860	.990	2.100	1.950	.910	8.810
2.	2.600	.975	1.820	1.755	.845	7.995
3.	1.625	.650	.980	1.040	.715	5.010
4.	3.250	.780	2.015	2.080	.910	9.035

Spines on legs apparently unnoteworthy; many are lost and scars are difficult to locate with certainty.

Abdomen. General features essentially as shown in Figures 13 and 14. Moderately flattened. With no anterior marginal spines; with a pair of lateral dorsal spines of moderate length; bifurcated posteriorly with each fork subdivided into two spines with the larger below.

Epigynum. Unlike that seen in any other species; anterior border of modified portion a granulated rim; features essentially as shown in Figures 15-17.

Color in alcohol. Legs and mouth parts a dull reddish brown, lighter beneath. Sternum light brownish. Carapace with a brownish central stripe and a broad dark brown stripe on each side (both represented by stippling in Figure 13); remainder of central region yellowish. Abdomen: irregularly yellowish white dorsally with nearly black margins; venter light yellowish from genital furrow to base and lateral sides of cone surrounding spinnerets; the cone with a nearly black circular ring; remainder of venter irregularly dark brown or black with yellowish spots and streaks. Probably some loss of coloration from long preservation.

Type locality. The holotype was simply labelled: Argentine, Sunchal, with no date of collection given. Apparently Cockerell was the collector. The species is named in honor of Dr. J. G. Sheals, Department of Zoology, British Museum (Natural History).

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Museum of Comparative Zoology

CAMBRIDGE, MASS. MARCH 11, 1960 NUMBER 122

NOTES ON CERTAIN SPECIES OF MICRATHENA (ARANEAE, ARGIOPIDAE) FROM SOUTH AMERICA

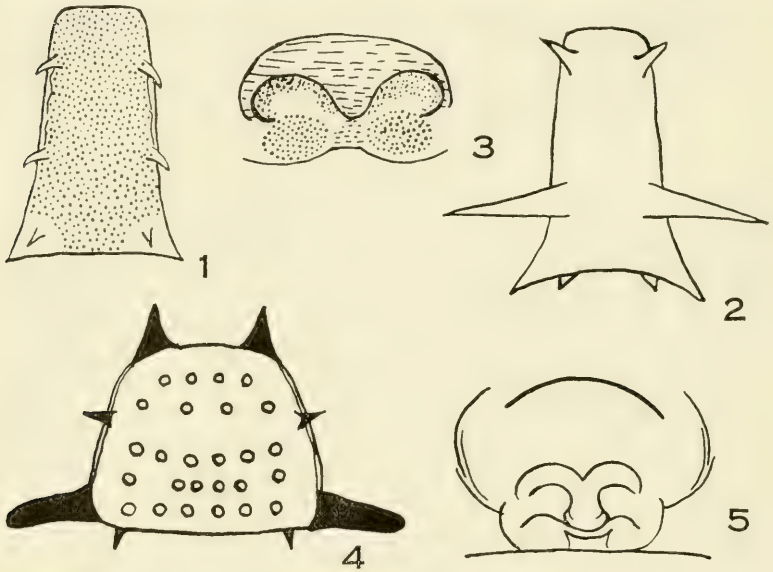
By ARTHUR M. CHICKERING
Albion College, Albion, Michigan

During a period of work in the Museum National d'Histoire Naturelle in Paris during the summer of 1958 Dr. Herbert W. Levi, Associate Curator of Arachnology in the Museum of Comparative Zoology at Harvard College, examined types of nine species of *Micrathena* Sundevall 1833, all originally described from South America by the great arachnologist, Eugène Simon. All of these species are poorly known and most of them have not appeared in collections since the originals were studied by their author. All were briefly described in 1896; four were mentioned in 1895 and accompanied by five simple figures. During the examination of the types mentioned Dr. Levi made free-hand drawings of the dorsal surface of the abdomens to show general form and spination. He also made careful drawings of the external genitalia when the latter were available; these were made with the use of a reticule with squares. All of the drawings made by Dr. Levi were turned over to the author to use as he saw fit in connection with his study of the genus. The figures appearing in this paper were made directly from Dr. Levi's original pencil drawings. The outline figures of abdomens are freehand copies with enlargement; the drawings of genitalia were made with tracing paper directly from Dr. Levi's originals. It has seemed worth while to present these data, thus obtained, with the hope that they will be of some help to others who may continue the study of this most interesting genus.

Micrathena aciculata Simon, 1897
(Figure 1)

M. aciculata Petrunkevitch, 1911
M. aciculata Roewer, 1942
M. aciculata Bonnet, 1957

The type is an immature female from Venezuela. Apparently the species has not been reported in collections since the original was taken. The general form of the abdomen with its spination,



External Anatomy of *Micrathena*

Figure 1, *M. aciculata*, abdomen, dorsal view.
Figures 2, 3. *M. gaujoni*, abdomen, dorsal view and epigynum, respectively.
Figures 4, 5. *M. hamifera*, abdomen, dorsal view and epigynum, respectively.

seen in dorsal view, is shown in Figure 1. The stippled area is black and the postero-lateral corners are white. The male is unknown.

Micrathena gaujoni Simon, 1897
(Figures 2, 3)

M. gaujoni Petrunkevitch, 1911
M. gaujoni Reimoser, 1917

M. gaujoni Roewer, 1942
M. gaujoni Bonnet, 1957

Simon stated that the type was 8.7 mm. long and similar to *M. fissispina* (C. Koch), but this hardly seems correct. There are four pairs of spines, the second pair the longest (Fig. 2). The epigynum has a pair of depressions directed posteriorly beneath an overhanging rim (Fig. 3). The type is from Ecuador and the male is unknown.

Micrathena hamifera Simon, 1897
(Figures 4, 5)

The length of the holotype was given as 9 mm. The general form of the abdomen with its spination is shown in Figure 4. The dorsal surface is like white enamel in general appearance. Figure 5 shows the form of the epigynum from "slightly behind"; just posterior to the curved boundary there is a large "sclerotized knob." The female is known only from Peru and the male is still unknown.

Micrathena imbellis Simon, 1895
(Figure 6)

M. imbellis Simon, 1897
M. imbellis Petrunkevitch, 1911
M. imbellis Reimoser, 1917
M. imbellis Roewer, 1942
M. imbellis Bonnet, 1957

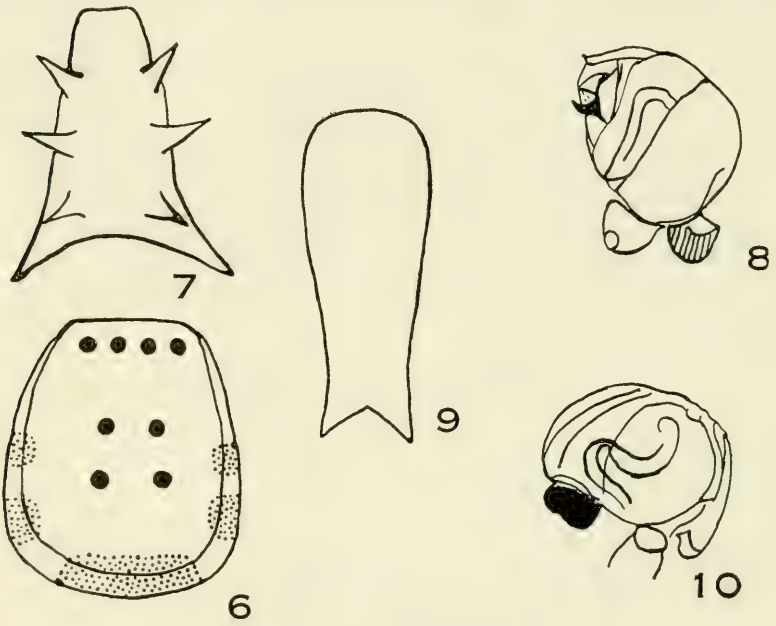
Simon (1895) included a figure showing the right side of the abdomen with no spines. Reimoser (1917) just mentioned the species and did not include it in his further treatment of the genus. The general appearance of the dorsal surface of the abdomen is shown in Figure 6; the stippled areas in the figure are black in the type. Dr. Levi has determined that the type is an immature female from Venezuela. The male is unknown.

Micrathena perlata Simon, 1895
(Figures 7, 8)

M. perlata Simon, 1897
M. perlata Petrunkevitch, 1911
M. perlata Reimoser, 1917

M. perlata Roewer, 1942
M. perlata Bonnet, 1957

The length of the female type is given as 6 mm. Dr. Levi has found that it also is immature. The general appearance of the dorsal surface of the abdomen is shown in Figure 7. The immature female is accompanied by a male which may or may not



External Anatomy of *Micrathena*

Figure 6. *M. imbellis*, abdomen, dorsal view.

Figures 7, 8. *M. perlata*, abdomen, dorsal view and male palp, respectively.

Figures 9, 10. *M. pubescens*, abdomen, dorsal view and male palp, respectively.

be properly paired with it. Figure 8 shows certain features of the palpal tarsus. The specimens are simply labelled "Amazon." Simon (1895) stated that the type came from: "Brasilia: S. Paulo de Olwenca (de Mathan)."

MICRATHENA PUBESCENS Simon, 1895
(Figures 9, 10)

M. pubescens Simon, 1897
M. pubescens Petrunkevitch, 1911
M. pubescens Reimoser, 1917
M. pubescens Roewer, 1942
M. pubescens Bonnet, 1957

The female type is immature. The abdomen is hairy and suggests a close relationship with *M. furcula* (O. P. Cambridge) from Central America. There are no true spines but the posterior end of the abdomen is somewhat bifurcate. Simon (1895) furnished figures to show the right side of the abdomen and the bifurcate posterior end. The immature female is accompanied by a mature male the palpal tarsus of which is shown in one position in Figure 10. Caution must always be exercised in matching the sexes in this genus and this male should be very carefully studied and compared with the growing number of different kinds of known males. The specimens are from Matto Grosso, Brazil.

MICRATHENA PUPA Simon, 1897
(Figures 11, 12)

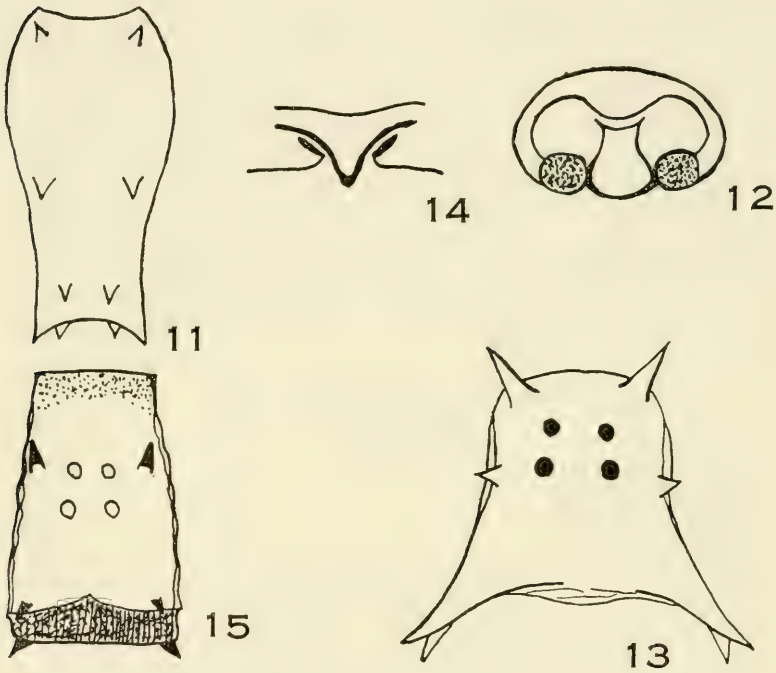
M. pupa Petrunkevitch, 1911
M. pupa Reimoser, 1917
M. pupa Roewer, 1942
M. pupa Bonnet, 1957

The length of the type is given as 8 mm. The form of the abdomen and its spination are shown in Figure 11 and some of the features of the epigynum in Figure 12. The type female is from Ecuador. Simon apparently had a male associated with the female but Dr. Levi did not find it in the collection. Presumably it is lost and the original description does not give what we now consider to be the important diagnostic male features.

MICRATHENA TOVARENSIS Simon, 1897
(Figures 13, 14)

M. tovarensis Petrunkevitch, 1911
M. tovarensis Reimoser, 1917
M. tovarensis Roewer, 1942
M. tovarensis Bonnet, 1957

The length of the female type is given as 7.8 mm. The general appearance of the abdomen and its spines, as seen in dorsal view, are shown in Figure 13. The appearance of the epigynum as shown in Dr. Levi's drawing is given in Figure 14. The type is from Venezuela. The male is unknown.



External Anatomy of *Micrathena*

Figures 11, 12. *M. pupa*, abdomen, dorsal view and epigynum, respectively.
Figures 13, 14. *M. tovarensis*, abdomen, dorsal view and epigynum, respectively.
Figure 15. *M. xanthopyga*, abdomen, dorsal view.

Micrathena xanthopyga Simon, 1895
(Figure 15)

M. xanthopyga Simon, 1897
M. xanthopyga Petrunkevitch, 1911

M. xanthopyga Reimoser, 1917
M. xanthopyga Roewer, 1942
M. xanthopyga Bonnet, 1957

The type is an immature female whose general appearance in dorsal view is shown in Figure 15. Simon (1895) published a figure of the type viewed from the right side. This figure shows four pairs of spines instead of three, as shown in Dr. Levi's drawing. The type is from Venezuela. The male is unknown.

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BREVIORA

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ALEPISAURUS BREVIROSTRIS, A NEW SPECIES OF LANCETFISH FROM THE WESTERN NORTH ATLANTIC

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Exploratory fishing for tunas in the western North Atlantic by the Fish and Wildlife Service vessel DELAWARE has revealed the presence of considerable numbers of lancetfishes, genus *Alepisaurus*. Through the courtesy of Mr. James L. Squire, I have been privileged to accompany most of these cruises. On the first two, the presence of *Alepisaurus* was recorded and stomach contents sampled, but only two specimens were saved. During the third cruise, it became apparent that two morphological types were represented, and from then on an attempt was made to measure and make counts on all possible specimens, and to preserve a large sample.

At first the possibility was entertained that the differences might be due to sexual dimorphism. Gonads were therefore examined on all preserved specimens and on a large number of fresh ones. The appearance was almost exactly the same in all specimens, indicating that sexual dimorphism was probably not a factor. This has been borne out by histological studies of the gonads, which lead me to the rather surprising conclusion that both morphological types, which I am now certain represent valid species, are hermaphroditic.

A study of nearly all type specimens and of all original descriptions leads to the conclusion that all previously described Atlantic species are conspecific with *A. ferox* Lowe. The second form is described here.

ALEPISAURUS BREVIROSTRIS, sp. nov.
(Figures 1-2)

Holotype. U. S. National Museum 186197, 682 mm. in standard length when fresh, 684 mm. preserved; taken on longline with 20-fathom buoy lines by the M/V DELAWARE at 38° 49′ N, 64° 02′ W, on September 13, 1957.

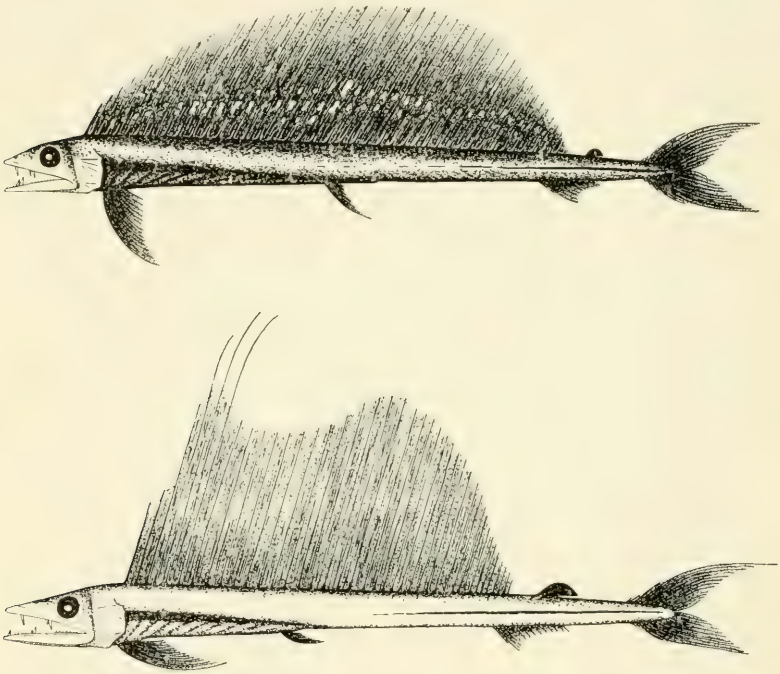

Figure 1. Left lateral view of *Alepisaurus brevirostris* (top), and *A. ferox* (bottom).

Paratypes have been distributed to the Museum of Comparative Zoology, Academy of Natural Sciences of Philadelphia, Cornell University, University of Miami Marine Laboratory, Tulane University, Scripps Institution of Oceanography, Stanford Natural History Museum, Museum of Zoology University

of Michigan, California Academy of Sciences, British Museum (Natural History), Museum National d'Histoire Naturelle Paris, and Museu Municipal do Funchal.

Diagnosis. A dark-hued species of *Alepisaurus* with a gradually arcuate dorsal fin profile, the dorsal origin well forward of the rearmost margin of the operculum, a short head (6.5 or more in standard length), and a short snout (2.5 or more in head).

Description. Dorsal fin high, originating over the middle of the opercle, its longest ray (about number 25-30) about three times the greatest depth of the body; its rays flexible, easily bent and broken, not branched, joints difficult to observe, though present. Leading dorsal ray thickened, its anterior edge finely serrated. Anal fin highest at the second and third rays, the rays branched distally. Pectoral fin pointed, its middle rays longest; first ray thickened, serrated anteriorly, unbranched, the rest branched and obviously jointed. Pelvic fin also pointed, the middle rays longest, the first ray thickened, serrated anteriorly, and unbranched, the remaining rays jointed and branched. Caudal fin strongly forked, with eight procurrent rays in each lobe, ten upper principal rays and nine lowers; uppermost principal rays considerably elongated in some specimens.

Snout inclined downward more sharply than the rear of the head, its length more than 2.5 times in head length. Nostrils a little less than halfway from tip of snout to anterior edge of orbit, the anterior opening round, the posterior crescent-shaped. Upper and lower jaws subequal. Upper jaw with a row of many small thin teeth on the premaxilla, one or two large fangs on anterior palatine, about three smaller fangs on the rear of the same bone, followed by about 7-10 low, triangular teeth. Lower jaw with an anterior large fang, followed by about 10 small caniniform teeth, one to three large fangs, and about 10-15 low, triangular teeth. No teeth on poorly developed tongue. Two patches of pharyngobranchial teeth. Gill arches with 3-6 upper, 0-1 middle, 17-23 lower groups of low, spinous rakers, totaling 23-28 groups. Branchiostegals mostly 7. Eye about 5 in head length, with vertical adipose eyelids anteriorly and posteriorly. Preopercle smooth. Opercle large, sculptured with lines radiating from its antero-dorsal corner; subopercle also with striae

radiating from its anterior point; interopercle apparently absent. Interorbital space bounded by prominent parietal ridges, the area forming a flat to slightly concave surface, gradually widening posteriorly.

Body elongate, its greatest depth, at level of pectoral fins, about 12 in standard length. A low lateral keel occupying most of the rear half of each side. Lateral-line pores opening along the keel and continuing forward beyond it; lateral line on head forming prominent supraorbital, suborbital, and preoperculomandibular systems; supratemporal apparently lacking. Anus posterior to pelvic insertion by less than half the length of the pelvic fins.

Fin-ray counts and morphometric data are given in Tables 1 and 2.

Coloration. Body iridescent brownish-black dorsally, becoming gradually lighter laterally. Region above lateral line liberally sprinkled with both large and small melanophores, many of the former ocellated. Below the lateral line, and particularly on the belly, many small melanophores present. General coloration decidedly dark in comparison with *A. ferox*. Lateral keel black. Dorsal fin membrane iridescent black, often with a horizontal row of white spots a short distance above base. Other fins, including adipose dorsal, black. Head dark above, becoming lighter ventrally. Abdominal cavity marked externally by alternating light and dark bands, the light ones representing strips of muscle, between which the dark peritoneal lining shows through.

Visceral Anatomy. Peritoneal lining black. Liver relatively small, covering only the most anterior portions of the stomach and intestine. Stomach black, highly distensible, forming a long, blind sac. Intestine arising at the anterior end of the stomach, continuing straight, without bends, to the anus, divided at about one-third of its length into anterior thick-walled and posterior thin-walled portions. Kidneys occupying the entire length of the body cavity, lying retroperitoneally along the ventral side of the vertebral column. Ureters enter a thin-walled urinary bladder which extends about from the level of the pelvic insertion to the anus. Gonads consisting of a prominent pair of elongate, continuous ovaries, which occupy the posterior third of the body

cavity above the intestine, and a pair of thin testes, almost invisible, lying in the dorsal groove formed by the two ovaries. The ducts of the ovaries, and presumably also those of the testes, join the urinary bladder and open by a urogenital pore immediately behind the anus. Swimbladder absent.

Related Species. Other than *A. brevirostris,* the only recognized Atlantic species of the genus *Alepisaurus* is *A. ferox* Lowe. The two species are distinguishable by many characters. The most trenchant ones are shown in Table 3, and may be visualized in Figures 1 and 2. In addition to these, many less-perfect ones are demonstrable. Characters associated with head length show significant differences (snout to dorsal origin, snout to pectoral insertion, see Table 2). The pectorals average about one-fifth of the standard length in *A. brevirostris* and are slightly shorter in *A. ferox.* The eye is relatively larger in *A. brevirostris,* doubtless correlated with the shorter snout. Meristic characters show consistent modal differences: dorsal rays most commonly 42-45 in *A. brevirostris,* 39-42 in *A. ferox;* anal rays usually 14-15 vs. 15-17; pelvic rays 13-14 vs. 14-15.

Alepisaurus is common in the Pacific, but at present it is not possible to ascertain the species. I have examined seven Pacific specimens in the U. S. National Museum and find them extremely similar to, if not conspecific with *A. ferox* (see Table 1). The only disconcerting element was the low number of dorsal rays in four specimens, which indicates at least some degree of differentiation. I have seen no examples of a form resembling *A. brevirostris* from the Pacific.

Young Specimens. Five specimens, 85.0 to 190.5 mm. standard length, present a confusing array of characters which defy positive identification. Tables 1 and 2 show for these specimens many characters within or beyond the ranges displayed by adults of both *A. brevirostris* and *A. ferox.* There is obviously a great change between 200 and 500 mm. in the relative proportions, the caudal end in particular increasing proportionally greatly in this time. Presumably the shape of the head also changes, as these five are all extreme, even to *A. brevirostris,* in having short heads and snouts. I am inclined to call them all *A. ferox,* but with considerable doubt.

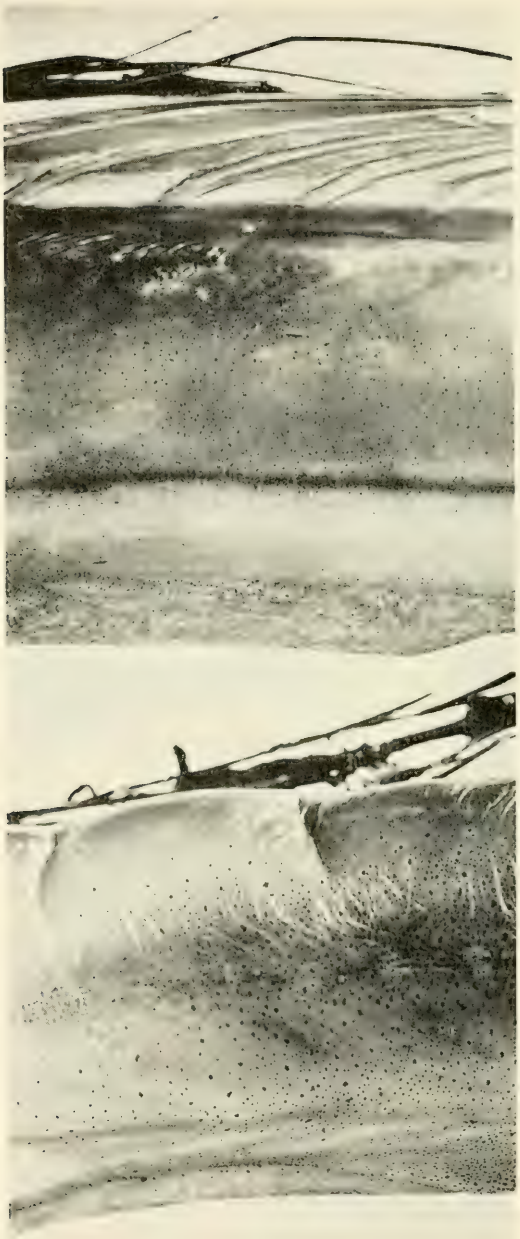

Figure 2. Photographs showing melanophore patterns of *A. brevirostris* (left), and *A. ferox* (right). Dorsal side to the right.

Mensural Discrepancies. Counts and a few selected measurements were made at sea on most of the specimens which came aboard the M/V DELAWARE. A later check has shown that the measurements cannot be used in conjunction with others taken on preserved specimens. Among the 17 preserved specimens of each species used in the descriptions here, were 11 *A. ferox* and 16 *A. brevirostris* which were also measured at sea when fresh. In these, the measurements of standard length and head length were consistently less in preserved specimens. In *A. ferox,* the standard length of one specimen was 0.7 per cent greater, the others 1.0-16.2 per cent less, averaging 6.6 per cent less. The head lengths were 3.4-6.6 per cent less, averaging 5.1 per cent. The corresponding figures for *A. brevirostris* were: standard length 0.3 and 1.1 per cent greater in two, others 2.0-13.1 per cent less, averaging 4.5 per cent less; head length 0.5-2.8 per cent greater in three, 0.5-9.2 per cent less in 13, averaging 2.7 per cent less.

Synonymy. Previous descriptions of *Alepisaurus* leave much to be desired. Eight nominal species have been described. I believe all these descriptions refer to a single, perhaps polytypic, species. These names are discussed below.

Alepisaurus ferox Lowe, 1833. The original description was made from two specimens from Madeira (Lowe, 1835a). In all important characteristics the written description is nearest *A. ferox* as recognized in the present study, but the accompanying drawing shows an arcuate dorsal fin profile, an absolute character of *A. brevirostris.* The matter was further complicated by a description and drawing of a third specimen from Madeira (Lowe, 1835b) which shows a dorsal fin profile characteristic of *A. ferox.*

N. B. Marshall has kindly examined two types in the British Museum. His observations leave no doubt that both are *A. ferox* as I understand it. In the specimen labeled "TYPES!" (no registered number) the standard length is 1125 mm., head length (to tip of lower jaw, as upper is damaged) 191 mm. (17%), dorsal rays 39 or 40, anal 17, pectorals 14. In the specimen labeled "SYNTYPE" (number 1852.9.13.98) the standard length is 1225 mm., head length 206 mm. (17%); snout 90 mm. (44% of head); dorsal 41, anal 17, pectorals 15. In both, the

dorsal origin is over or slightly behind the posterior edge of the operculum and no large, ocellated melanophores are present; both are larger than any *A. brevirostris* I have seen. The name *Alepisaurus ferox* is thus reasonably established for the long-snouted species.

Alepisaurus azureus Valenciennes, 1849. No type is extant, but the following parts of the original description strongly suggest *A. ferox:* ". . . la dorsale est d'égale hauteur jusque vers le trentième rayon . . ." (Cuvier and Valenciennes, 1849: 531); dorsal rays 38, anal 16. The pectoral count of 10 is presumably in error. The length of 5 feet 3 inches is larger than any known *A. brevirostris.* The description was based on a specimen from the Canary Islands.

Alepisaurus richardsonii Bleeker, 1855. Based on the description by Sir John Richardson (1844) of a head from Van Diemens Land. The drawing of the head shows a snout most like *A. ferox.*

Alepisaurus altivelis Poey, 1861. It is difficult to be certain of this description. The anterior rays are all said to be the same height, the posterior ones decreasing rapidly; dorsal rays 40, anal 17, pectorals 16; all most like *A. ferox.* The pelvic count of 13 is presumably in error. Based on a Cuban specimen.

Alepidosaurus borealis Gill, 1863. Based on a head, dorsal, caudal, and pelvic fins from a Pacific specimen. I have examined this specimen and find it close to *A. ferox* except for a dorsal count of 35. The pelvic count of 13 is apparently an error. The stated snout/head ratio of 2/5 definitely precludes *A. brevirostris.*

Alepidosaurus serra Gill, 1863. Described from a head, caudal, and pelvic fins of a Pacific specimen. I can detect no significant differences between Gill's descriptions of this species and of *A. borealis.* He places much emphasis on opercular sculpturing, which seems to be quite variable and not a good specific character. Again the pelvic count of 13 is presumed to be an error. The distance from eye to snout, stated as 2/5 of head length, excludes *A. brevirostris.*

Alepidosaurus poeyi Gill, 1863. Described on the basis of drawings (which I have not seen) of the second specimen from Cuba mentioned by Poey (1861) in his description of *A. altivelis.*

The specimen was described as having the first dorsal rays becoming longer, the fourth very long, rays 6-24 high and equal. This suggests *A. ferox*, as does the dorsal ray count of 41. Poey's presumably erroneous pelvic count of 13 is restated.

Alepidosaurus aesculapius Bean, 1883. I have examined the type and find it similar to *A. ferox*. The dorsal rays could not be counted accurately, but Bean (1883) gave 39; anal rays 16, both *A. ferox* characters. The snout length (41% of head length) rules out *A. brevirostris* with absolute certainty. Described from a Pacific specimen.

Distribution of Alepisaurus in the Atlantic. Among the specimens examined and definitely identified, the most southerly was one *A. ferox* from off southern Puerto Rico, now in the Museum of the University of Miami Marine Laboratory. Several of the same species from the Gulf of Mexico are in the U. S. National Museum, and specimens from the Gulf of Maine (La Have Bank the most northerly) were seen at the Museum of Comparative Zoology. The remaining positively identified specimens of *A. ferox* and all those of *A. brevirostris* are from the region of the Gulf Stream (*sensu stricto*), almost all collected by the M/V DELAWARE. Some authors have documented their records well enough so that *Alepisaurus ferox* can be said with certainty to be found in the following additional regions: Madeira (Lowe, 1835a; Maul 1946); Canary Islands (Cuvier and Valenciennes, 1849); Cuba (Poey, 1861); coast of North Carolina (Brimley, 1938; also a specimen in the U. S. National Museum); Greenland, Iceland, Faroes (Jensen, 1948).

In the long-lining activities of the M/V DELAWARE, both species were taken on the same set on several occasions. Surface temperatures at stations at which *A. ferox* were taken ranged from 69-83°F, for *A. brevirostris* 58-84°F. The buoy lines, attached to the end of each section of long-line gear, have been 10-20 fathoms long, mainly the latter; the specimens have thus been taken quite near the surface. It is noteworthy that, while *A. ferox* and *A. brevirostris* have been taken in good numbers in late summer and fall, they have been extremely scarce in June. The only spring specimen still available, though many were taken, turned out to be *A. brevirostris*. Only *A. ferox* was taken in winter.

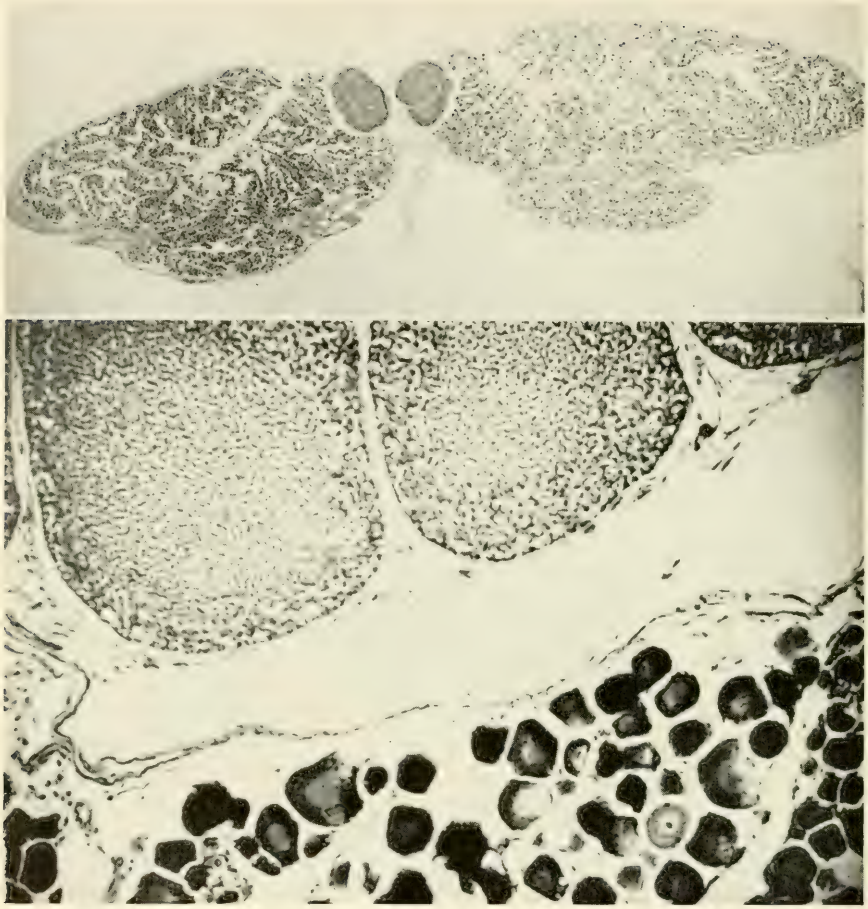

Figure 3. Gonads of *Alepisaurus ferox*, typical of both species. Top: cross-section through entire structure, testes the small, lobular structures in center. Bottom: enlargement showing two lobules of testis above and darkly-stained eggs below.

Reproductive Condition. When the possibility was being considered that the two species of *Alepisaurus* might be dimorphic sexes, gonads were immediately examined on all available specimens, and all others possible were thereafter inspected at sea and

many were preserved. All appeared to be immature females. No specimens even approaching ripeness have yet been seen.

Results of histological examination have shown the surprising fact that both male and female gonadal structures are present in both species (Fig. 3). The testes lie dorsal to the much-larger ovaries and in the groove between them. The ducts of both organs appear to unite before reaching the urogenital opening. When the testes are examined under oil immersion, meiotic activity is visible in peripheral cells of the crypts in spite of poor fixation. The eggs of the ovaries are fairly well-developed. The conclusion can hardly be escaped, therefore, that both species of *Alepisaurus* are hermaphroditic.

ACKNOWLEDGMENTS

I am particularly indebted to James L. Squire, chief of North Atlantic Fishery Exploration and Gear Research of the U. S. Bureau of Commercial Fisheries and to field personnel and members of the crew of the M/V DELAWARE for many courtesies rendered in connection with the exploratory cruises of the DELAWARE. Specimens at the U. S. National Museum, Museum of Comparative Zoology, and the Museum of the University of Miami Marine Laboratory were examined through the kindness of Giles W. Mead, Myvanwy M. Dick, and C. Richard Robins. I have profited from correspondence or discussions with Norman J. Wilimovsky, Giles W. Mead, and G. E. Maul. My sincere appreciation goes to M. Blanc of the Museum d'Histoire Naturelle in Paris for his efforts in assuring the lack of types there and to N. B. Marshall for information on the types of Lowe in the British Museum. Gail G. Pasley of Woods Hole Oceanographic Institution made the full-length drawings.

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Table 1. Fin-ray and gill-raker counts of *Alepisaurus*

	Dorsal Rays															Pelvic Rays		
	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	8	9	10
A. brevirostris							3	1	3	5	4	6	1	1	1	1	19	3
A. ferox			2		3	10	10	10	7	4	2	1				2	43	7
Pacific (USNM)	2	2				1			1							3	3	
Small								1								1	3	1

	Anal Rays						Pectoral Rays					Gill Rakers						
	13	14	15	16	17	18	12	13	14	15	16	23	24	25	26	27	28	29
A. brevirostris	1	9	12	1			1	13	10			2	3	4	1	1	3	2
A. ferox		1	14	21	15	1	1	5	30	16		1	4	4	5	2	1	
Pacific (USNM)				6	1			4	3									
Small			3	2					2	2	1							

Table 2. Proportional dimensions of *Alepisaurus* expressed as per cent of standard length. Range, with mean in parentheses. Based on seventeen adult specimens of each species and five small specimens.

	brevirostris	*ferox*	small
Standard length, mm.	551-894(670.6)	431-1088(777.5)	85.0-190.5(144.2)
Per cent of standard length			
Snout to anal origin	77-83(79.5)	76-88(80.1)	80-81(80.0)
Snout to pelvic insertion	42-50(46.3)	43-53(47.5)	53-58(55.3)
Snout to pectoral insert	13-16(14.7)	17-23(19.4)	22-25(24.0)
Snout to dorsal origin	9.4-13(11.4)	16-22(17.9)	21-25(23.2)
Head length	12-16(14.5)	16-23(18.6)	23-30(25.6)
Greatest depth	7.2-10.4(8.5)	8.0-12.5(9.5)	13-16(14.4)
Caudal peduncle depth	1.9-3.2(2.4)	2.3-4.0(2.8)	2.7-4.0(3.4)
Pectoral length	14-20(16.3)	17-24(20.5)	15-19(17.3)
Pelvic length	7.2-12.4(9.5)	7.5-10.4(9.0)	7.4-8.5(7.9)
Anal base	8.5-11.4(9.8)	9.2-13.8(10.7)	9.5-13(11.1)
Anal height	5.9-7.9(6.9)	7.4-10.3(8.6)	6.5-9.1(7.8)
Per cent of head length			
Snout to fleshy orbit	31-37(34.5)	41-46(43.3)	36-41(38.4)
Snout to bony orbit	26-31(28.4)	35-42(38.1)	27-37(31.4)
Fleshy orbit length	19-23(20.9)	13-20(17.8)	25-28(26.2)
Bony orbit length	23-33(27.8)	17-28(23.4)	31-36(33.4)
Least interorbital width	15-20(17.5)	14-18(16.2)	15-17(16)
Snout to anterior nostril	14-16(14.9)	21-24(22.4)	14-18(17.2)
Number of gill raker groups (total)	23-28(25.4)	23-29(25.8)	25-27(26)

Table 3. Principal differential characters of *A. brevirostris* and *A. ferox*

A. brevirostris	*A. ferox*
Coloration dark, more and larger melanophores, many of them ocellated (Fig. 2)	Coloration light, fewer, mostly small melanophores, few or none ocellated (Fig. 2)
Dorsal fin gradually arcuate, without free anterior rays (Fig. 1)	Dorsal fin with several anterior rays elongated, free from membrane; rest of fin about equal in height until sudden posterior drop, or slightly higher before drop (Fig. 1)
Irregular horizontal row of white spots often present on dorsal membrane	No white spots on dorsal membrane
Dorsal origin well in advance of rear margin of the operculum	Dorsal origin about level with the rear margin of the operculum
Head 6.5 or more in standard length	Head less than 6.5 in standard length
Snout 2.5 or more in head length	Snout less than 2.5 in head length

BREVIORA

Museum of Comparative Zoology

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ANISIAN AMMONOIDS FROM MALAYA

By BERNHARD KUMMEL

Fossiliferous marine strata are sparsely represented or known from Malaya. Even the Triassic system which is one of the better known systems to yield fossils is represented by extremely small faunas consisting mainly of pelecypods, and only indeterminate ammonoids have been reported by Newton (1923, 1925). The first discovery of determinable ammonoids was reported by Savage (1950) from mudstones near Kuala Lipis, Pahang. The initial collections were submitted to L. F. Spath of the British Museum (Natural History) who made the following report (in Savage, 1950): "Quite a number of common Middle Triassic (Anisian) genera can be recognized in the collection, including *Paraceratites* (dominant), *Sturia*, *Ptychites*, and *Acrochordiceras*, so that the age of the assemblage is the *trinodosus* zone. Specific identifications would be more difficult but are unnecessary: *Paraceratites trinodosus* (Mojsisovics) and such close allies as the Himalayan *Ceratites thuilleri* (Oppel) and *P. winterbottomi* (Salter) are probably all represented."

The rarity of Triassic ammonoids in Southeast Asia, lying as it does at the eastern end of Tethys between the richly fossiliferous Triassic horizons of the Himalayas and the island of Timor, warrants a more substantial record of these faunas than Spath was able to give. Through the kindness of Dr. M. K. Howarth of the British Museum (Natural History) all of the best preserved material from Kuala Lipis, Pahang, was loaned to the writer. Close examination of this small collection (29 specimens) showed that Spath's conclusions as to genera present and age assignment are correct in spite of the rather poor preservation.

The fauna contains the following species:

Paraceratites trinodosus (Mojsisovics)
Sturia sansovinii Mojsisovics
Acrochordiceras sp. indet.
Ptychites sp. indet.

Data on the geographic and geologic occurrence of this fauna can best be quoted from Savage (1950, p. 76): "One of the newly recorded areas is some 10.5 miles south-south-west of Kuala Lipis on one of the branches of the Sungei (= River) Tua, where it flows through Budu Estate (approximately lat. N. 4°02′30″, long. E. 102°00′15″; Malayan Survey Department Topographical Sheet No. 2 0/13). The rocks are mudstones, rarely laminated sufficiently to be called shales. They are fairly homogeneous, slate grey, almost black and carbonaceous; but some slightly sandier strata (muddy siltstones) weather to a pale buff or brown. The beds show minor flexures but in the main strike 40°-220° and dip to the north-west at angles of about 40°. They are strongly jointed along several directions, the two main joint systems being vertical and striking 60°-240° and 155°-335°. The beds are fossiliferous over a distance of at least 50 yds. in a horizontal direction normal to the strike, equivalent to a stratigraphical thickness of about 100 ft." No data are available with the specimens as to their precise position in the fossiliferous horizon.

The species recognized in this small fauna are common forms widely distributed in Tethys and the general circum-Pacific region. *Paraceratites trinodosus* and *Sturia sansovinii* were originally established on Alpine specimens. The specimens assigned to *Ptychites* and *Acrochordiceras* are too poorly preserved to enable specific identification but there is no doubt as to the generic assignment.

The two previous records of Triassic ammonoids from Malaya are not as satisfactory. A small fragment of an ammonoid was recorded by Newton (1923, p. 302, pl. 9, fig. 29); it is quite indeterminable. The specimen came from argillaceous sandstone at Mount Faber, Singapore, and was reported to have a "depressed whorl with indications of straight ribs and furrows connecting with some well-separated knob-like tubercles situated within a short distance of the inner margin." Newton likewise

did not believe the specimen was determinable but thought that it resembled the genus *Balatonites*. There does not appear to be any justification for this suggestion. The second record of ammonoid remains from Malaya is also in a paper by Newton (1925) on a small Upper Triassic fauna from the Province of Kedah. The first of the two specimens available to Newton was cited as *Ammonites* sp. indet. "A" and he suggested that it may be referred to a form of the Arcestidae. It seems more likely that it is a *Juvavites* or possibly an *Anatomites* but the specimen lacks the characteristic constrictions of these genera (Spath, 1951, p. 106, footnote). The second specimen was listed by Newton as *Ammonites* sp. indet. "B" and suggested a resemblance to *Balatonites*. Spath (1951, p. 15) thought that this specimen might be *Hannoceras nasturtium* (Mojsisovics).

In the adjoining regions of southeast Asia only Indochina has yielded a large and varied fauna of Triassic ammonoids which, however, are generally not well preserved. The literature on the stratigraphy and faunas of this area is very large and need not be reviewed here. A brief summary can be found in Saurin (1956). The only other really new discovery of Triassic ammonoids in southeast Asia has been made in Thailand where Anisian and Karnian faunas are now known. The geology of this Triassic region has been described by Pitakpaivan (1955) who includes a preliminary list of the species present, identified by Kummel. Full description of this fauna will be published shortly.

In the following description of the species from Kuala Lipis the extensive synonymies for *Paraceratites trinodosus* and *Sturia sansovinii* have been omitted; essentially complete synonymies can be found in Diener (1915a) and Kutassy (1933).

SYSTEMATIC DESCRIPTIONS

Family CERATITIDAE Mojsisovics, 1879

Genus PARACERATITES Hyatt, 1900

PARACERATITES TRINODOSUS (Mojsisovics)

Plate 1, figures 3-6

The collection contains no less than twenty crushed and incomplete specimens that can be assigned to the well known

Paraceratites trinodosus (Mojsisovics). Allowing for the general faulty preservation, these specimens agree well in most details with the type of this species and with other specimens assigned to it. In his preliminary examination of the fauna, Spath (in Savage, 1950, p. 76) considered that in addition to *Paraceratites trinodosus* the fauna also contained *P. thuilleri* (Oppel) and *P. winterbottomi* (Salter). These are very closely allied forms occurring with *P. trinodosus* in the Himalayas. However, considering the poor preservation of the specimens, it seems that a more conservative approach is desirable and I am recognizing only the better known and more widely distributed *P. trinodosus*.

This species is particularly widespread in the Alps, Balkans and the Middle East. It is likewise recorded from the Himalayas and Nevada. Identical or closely related species are also known from Japan. This species gives its name to the upper Anisian *trinodosus* zone.

Repository. BMNH — C 55672, C 55673, C 55674, C 55675 (figured specimens); C 55653, C 55654, C 55655, C 55657, C 55658, C 55661, C 55662, C 55663, C 55666, C 55667, C 55668, C 55670, C 55671, C 55676, C 55678.

Family PTYCHITIDAE Mojsisovics, 1882

Genus Ptychitites Mojsisovics, 1875

Ptychites sp. indet.

Plate 1, figure 7

The collection contains three crushed and fragmentary specimens that without question belong in *Ptychites* but identification at the specific level is not possible nor advisable. The most complete specimen is actually only the impression of one side of a conch. The illustration on Plate 1, figure 7 is of a latex cast of this impression. It shows the funnel-shaped umbilicus, broadly arched lateral areas, and the radial ribs — all features which are very characteristic of the genus *Ptychites*.

Ptychites is known from Middle Triassic strata throughout the world. It likewise includes a very large number of species based largely on differences in shape of the conch, character of ribs, degree of involution, and details of the suture. In the Himalayan

Muschelkalk, *Ptychites*, of the group of *P. rugiferus* (Oppel) to which these Malayan specimens most likely belong, is one of the most abundant forms present, being represented by seven species (Diener, 1895, 1907). In southeast Asia the record of *Ptychites* is very fragmentary and represented mostly by indeterminate species. Even the rich Middle Triassic faunas of Timor appear to have only one species, *P. amarassicus* Welter (1915; Arthaber, 1928). The genus is, however, also present in Thailand and Indochina. It is also known to be present in Japan and New Zealand.

Repository: BMNH — C 55659 (figured specimen); C 55664, C 55656.

Genus Sturia Mojsisovics, 1882

Sturia sansovinii Mojsisovics

Plate 1, figure 2

The most easily recognizable species in the collection is this strigate form which is widely distributed throughout Tethys. The specimen consists only of the impression of slightly more than one third volution of one side of a whorl; no suture or whorl section is preserved. In spite of this fragmentary preservation the ornamentation is so characteristic that there is no reason to doubt its identity with this species. The ornamentation consists of broad, flattened strigations separated by broader, rounded grooves which bear a fine spiral line down the center. The pattern of ornamentation on the Malayan specimen is identical to the fine specimen from the Shalshal Cliffs in the Himalayas, figured and described by Diener (1895, pp. 61-62, pl. 15, figs. 1a, b). In his description of the Himalayan specimen Diener was quite emphatic as to the identity of his form with the type from the Alpine Middle Triassic. In this conclusion he had confirmation from Mojsisovics who also examined the Himalayan specimen.

Sturia sansovinii is known from Anisian and Ladinian strata at many localities in the Mediterranean region. Bibliographic citations to these can be found in Diener (1915a) and Kutassy (1933). The distribution in the region of eastern Tethys and in the circum-Pacific region is not so well known and is of special

interest here. This species is the only form of *Sturia* from the Himalayas proper in the so-called Himalayan facies, where Diener (1895, 1907) has recorded specimens from the upper Muschelkalk at the Shalshal Cliff and at Spiti. However, in Tibet in some of the exotic blocks of Malla Johar near Chitichun Peak No. 1 (17,740 ft.), Diener obtained a specimen of *Sturia* which he identified as *Sturia monogolica* (Diener, 1895, p. 113, pl. 29, fig. 4). This form is quite distinct from other species of *Sturia* in its open umbilicus and the suture, characterized by long, slender, pyramidal saddles. At a later date Diener (1916) erected the genus *Psilosturia* with *S. mongolica* as the type species.

Indeterminate species have been recorded from Middle Triassic horizons in upper Thailand (Kummel, in Pitakpaivan, 1955). These particular forms are small, poorly preserved, and crushed specimens whose relationship to *S. sansovinii* is impossible to determine. Among the numerous Middle Triassic faunas described from Indochina, *Sturia* has as yet not been recorded. Welter (1915) records *S.* cf. *sansovinii* from a Ladinian horizon on Timor based on a fragmentary specimen.

Sturia japonica Diener (1915b, pp. 18-20, pl. 6, figs. 1-2) is based on a highly distorted specimen from Middle Triassic formations at Inai, Japan. It is quite similar to *S. sansovinii* differing in minor features of the suture and character of the strigations.

Sturia sansovinii is thus found widely distributed throughout the Tethyan geosyncline where it occurs in strata of Anisian and Ladinian age.

Repository: BMNH — C 55669 (figured specimen).

Family ACROCHORDICERATIDAE Arthaber, 1911

Genus Acrochordiceras Hyatt, 1877

Acrochordiceras sp. indet.

Plate 1, figure 1

A single, large, crushed and elongated specimen can be assigned to the genus *Acrochordiceras* but its poor and incomplete preservation prevents determination of its specific relationship. The whorl sides bear strong radial to slightly curved sharp ribs.

Some of the ribs begin at the umbilical shoulders where they increase in height forming somewhat of a tubercle beyond which they bifurcate. Other ribs lack the umbilical protuberances and are slightly less prominent. The poor preservation prevents determining the pattern of alternation of these two types of ribs. The conch was no doubt slightly evolute but the shape of the whorl section is not possible to determine nor is any part of the suture preserved.

Close comparison of this Malayan specimen with the known species of *Acrochordiceras* is not very satisfactory but one feature is notable — that is, the rather sharp ribs on the Malayan form. The extent to which these sharp ribs may be due to the deformation of the specimen is hard to determine, however. In most species of *Acrochordiceras* the ribs tend to be rounded and in some cases broadly rounded. Even though specific comparisons are not possible there is no question of the generic assignment of this form.

The genus *Acrochordiceras* is widely distributed in the Tethyan belt from the Alps to Timor and is likewise known from a number of localities in the circum-Pacific region.

Repository. BMNH — C 55660 (figured specimen).

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Explanation of PLATE

The specimens illustrated on this plate are from mudstones of Anisian age from near Kuala Lipis, Pahang, Malaya. They are deposited in the British Museum (Natural History), London.

Figure 1. *Acrochordiceras* sp. indet. BMNH — C 55660. X 0.5.

Figure 2. *Sturia sansovinii* Mojsisovics. BMNH — C 55669. X 0.5.

Figure 3-6. *Paraceratites trinodosus* (Mojsisovics) BMNH — C 55672 — C 55675. X 1.

Figure 7. *Ptychites* sp. indet. BMNH — C 55659. X 1.

PLATE

BREVIORA

Museum of Comparative Zoology

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THE LUMINOUS ORGANS OF *PROCTOPORUS* (SAURIA, REPTILIA) — A RE-EVALUATION

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INTRODUCTION

The herpetological literature contains two reports describing the first luminous organs in a terrestrial vertebrate. The two papers discuss identical specimens of the Trinidad lizard *Proctoporus shrevei* Parker. Sanderson (1939, and observations cited by Parker, same date) claimed that light was emitted by black bordered ocelli on the sides of a male, and Parker (1939) supported this on the basis of his histological examination of the preserved animal.

No new observations have been published since that time, but a number of workers have commented upon the original observations. Thus Pope (1955, p. 306) remarked that "other teiids have spots somewhat like those of *P. shrevei*, so it is highly probable that they, too, can light up." In contrast to this, Harvey (1952, p. 494) in his monograph on bioluminescence stated that he believed "all reports of luminescence in higher vertebrates to be false or spurious due to reflection of light or infection by luminous bacteria."

The divergence of opinion on this interesting point prompted a re-examination of this question. The present paper reports a few additional field observations, and includes as well a detailed examination of the histological structure of the ocelli. Since *Proctoporus shrevei* is very rare, this re-examination had to be carried out on two related and superficially similar forms.

OBSERVATIONS ON LIVING SPECIMENS

Parker (1939, p. 659) mentioned that Sanderson's field notes contained only a brief reference to color pattern involving "five, black spots each containing a small, vivid white, sometimes luminous bead." Parker further stated that Sanderson in conversation informed him "that the animal was kept alive in captivity and could be stimulated to emit light from the lateral spots; the light was of a pale greenish hue, similar to that produced by the hands and figures of a luminous watch. Excitement produced by flashing an intermittent beam of light on the lizard was found to be a very effective stimulus to light production."

A more specific first-hand report was given by Sanderson (1939, pp. 41-43) in his popular, considerably amplified and slightly different, account. When initially observed the lizard "turned its head away from me and both its sides lit up for a few seconds like the portholes of a ship." "After one brilliant display on the night of its arrival in camp it refused to shine with full brightness though the beadlike spots remained plainly discernible in a darkened box when the rest of the animal was invisible." A "loud whistle, sudden winds, and flashes of light greatly agitated our lizard, causing it to switch on its "portholes". . . . The light was much brighter the first time it was switched on after the animal had been quiescent for a period, and more especially after it (the lizard) had previously been subjected to intense illumination."

We have been able to obtain four sets of further observations on live specimens of the genus *Proctoporus*.

Julian S. Kenny (V. C. Quesnel, personal communication) some time ago repeated Sanderson's experiments on the original species (*P. shrevei*) with entirely negative results. Kenny's field notes also indicate that the lizards are diurnal and inhabit relatively open spaces on El Tucuche, Trinidad.

Dr. Janis Roze (*in litt.*) states that a specimen of *Proctoporus achlyens* Uzzell (M.C.Z. 53128, later used for histological examination reported herein) did not glow when placed in a darkened room after capture. He adds that exposure to ultraviolet light did cause the spots to shine faintly. The test was carried out in an incompletely darkened room, and the results seem to be open to some question.

Harold Heatwole and Owen J. Sexton (personal communication) performed a number of experiments at a field station in Venezuela. They tested one adult male of *P. luctuosus* (Peters)

and two adult males of *P. achlyens* for a period of one month. The spots of the first species were yellow and those of the second were red in life, both series of spots bleaching to white after formalin preservation. The specimens were repeatedly moved from light to dark environments and were observed at night. The animals were disturbed. No luminescent effect was ever noted. Ultraviolet illumination was not attempted.

The most extensive series of observations on live animals was made in Ecuador by James A. Peters (*in litt.*). Specimens of *Prionodactylus vertebralis* (O'Shaughnessy) and *Neusticurus ecpleopus* Cope were observed while free in the field, during the collecting process, and for several weeks in the laboratory. He reported that neither luminescence nor any other kind of light could be noted in broad sunlight, dim or artificial light, or in the complete absence of light. No reflection could be noted under various types of lighting (sun, fluorescent and incandescent), in quiescent, active or deliberately disturbed animals. The evidence is most valuable because Peters was aware of the lizards' reputation and was deliberately testing the hypothesis of luminescence.

SUPERFICIAL APPEARANCE AND PHYLOGENETIC DISTRIBUTION OF THE OCELLI

The supposedly luminous ocelli (Fig. 1) are rather similar in the species of *Proctoporus* and *Neusticurus* here discussed. They are arranged in a single row along the side of the animal; each ocellus always shows a light-colored, sharply-defined, black-bordered, circular center. They may be restricted to adult males, with juvenile specimens and females showing only traces. There is usually a size decrease of the ocellar center posteriorly along the series. There may be a marked irregularity in the width of the black border. There is no correlation between the ocellar and the scale patterns.

While sharply-defined ocelli are commonly well developed only in Boulenger's (1885, p. 332) teiid group II, a check of the more than 130 species of teiid lizards as well as forms of other families represented in the collection of the Museum of Comparative Zoology at Harvard College indicated that patterns with sharply contrasting light and dark colors are extremely common. A complete morphological series may be demonstrated in the Teiidae. This series ranges from patterns with alternating light and dark stripes, through those in which the stripes alternately fuse and break up, to patterns with well-defined light circles on

a dark background. Such spots may be found over the entire body or may be restricted to the sides. The condition found in the males of *Proctoporus* and *Neusticurus* represents only one extreme development of color variation. Similar conditions may also be observed in certain geckonids and iguanids. Here the ocellar pattern may occur all along the side, with the color contrast emphasized around a limited number of spots.

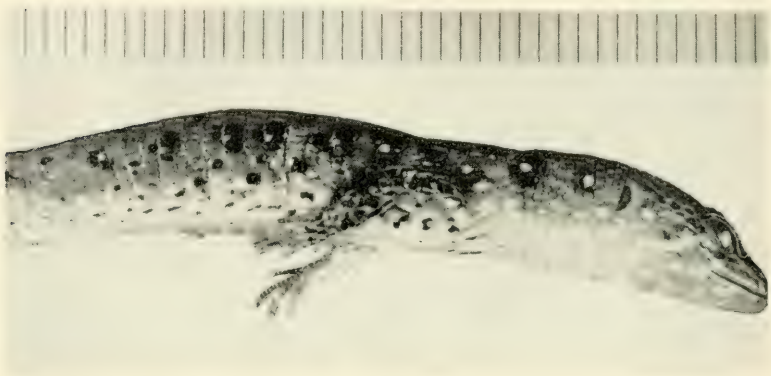

Fig. 1. *Proctoporus achlyens* Uzzell. Lateral view to show shape, size and arrangement of ocelli. The scale is graduated in mm. (M.C.Z. 53128 — C.G. photo.)

HISTOLOGICAL AND HISTOCHEMICAL EXAMINATION OF THE SKIN

Methods

Two specimens were used for histological examination. These were M.C.Z. 43764, *Neusticurus ecpleopus ocellatus* Sinitzen from Hacienda Pampayacu, Departamento de Huanuco, Peru, and M.C.Z. 53128, *Proctoporus achlyens* Uzzell from Choroni, Estado de Aragua, Venezuela. The museum specimens were reported to have been fixed in 10 per cent formalin and transferred to 70 per cent alcohol for storage.

Sections were cut from the second (and largest) ocellus of the left side of each specimen. A sample of faintly pigmented skin from the ventral surface of M.C.Z. 53128 was sectioned for comparison. Small blocks of tissue, including both the center and the black margin, in the case of the ocelli, were excised. These tissue blocks, including the epidermis, dermis, and a small amount of underlying skeletal muscle were hydrated through a

descending alcohol series, post-chromated in saturated aqueous potassium dichromate at room temperature for three days, washed overnight in running tap water, dehydrated in ethanol, cleared in chloroform, and embedded in tissue mat (56-58°). Five-micron sections were mounted individually so that various staining techniques could be carried out on adjacent sections.

The techniques used were: Harris hematoxylin and eosin and the paraldehyde fuchsin method as modified by Halmi (Halmi, 1950) for general morphology, Wilder's modification of the Bielchowsky silver impregnation method (Romeis, 1948, p. 355) for nerve fibers and endings, Sudan black B with acetone controls for lipid compounds, the periodic acid-Schiff technique for 1-2 glycol linkages, the azo dye methods for protein bound sulfhydryl and disulfide groups (Barrnett and Seligman, 1952, 1954), dilute methylene blue at pH's 4 to 9 and dilute light green at pH's 3 to 8 for a rough approximation of pH signature of proteins (Singer, 1952) and buffered toluidine blue and thionine for metachromasia.

GENERAL MORPHOLOGY OF THE SKIN AND OCELLUS

On the basis of the appearance of nuclei, blood cells, striated muscle fibers, small nerves, and the cells of the epidermis, the fixation was judged to be good. Presumably the external location of the tissue with the consequent immediate exposure to the formalin had been advantageous. In addition, the tanning with dichromate seems to have been successful in preventing the shrinkage that normally results from paraffin embedding of formalin-fixed tissues.

As revealed by hematoxylin and eosin (Figs. 2, 3), the epidermis is composed of a very thin stratified squamous epithelium showing a prominent basement membrane. The epithelium consists of a single-layered cuboidal stratum germinativum covered by only one or two layers of flattened squamous cells. The surface is covered by dense keratinous scales.

The dermis can be subdivided into two layers. Superficially, it is composed of a rather loose fibroelastic tissue which contains a dense accumulation of melanin pigment except in the region of the ocellus. The pigment appears to be contained in chromatophores, but this cannot be stated categorically for all of it. Often fine strands of pigment granules extend into the epidermis. In some instances these granules seem to be in processes between the epidermal cells, but in others they seem to occur within the

cytoplasm of the epithelial cells. Possibly they occur in both locations. The deep layer of the dermis is composed of typical dense collagenous connective tissue with a rather regular orientation parallel to the surface of the skin. Both layers of the dermis contain an extensive network of elastic and reticular fibers.

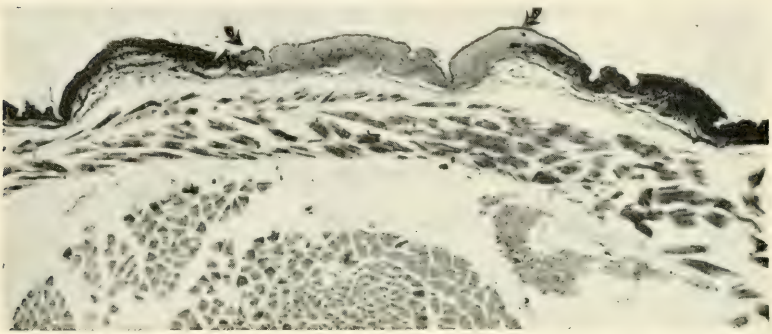

Fig. 2. Cross-section through the center of ocellus (between the arrows) and surrounding pigmented skin taken from *Proctoporus achlyens* Uzzell. Hematoxylin and eosin. 50X.

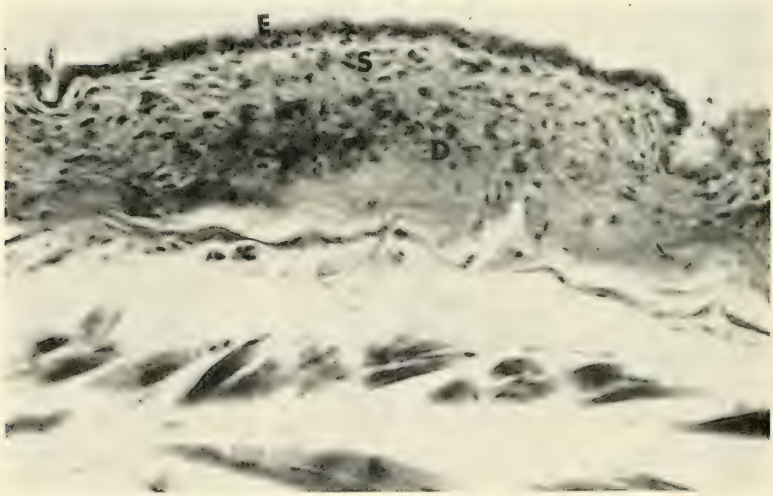

Fig. 3. Cross-section through the center of the ocellus shown in Fig. 2. Note the thin epidermis (E), the vacuolated appearance of the superficial layer of the dermis (S), and the dense collagenous deep layer of the dermis (D). Hematoxylin and eosin. 400X.

The dermis is underlain by typical loose connective tissue containing small blood vessels, fat cells, and small peripheral nerves.

The white center of the ocellus, which is the prime object of this study, differs histologically from the rest of the skin only in the fact that no melanin pigment occurs in the superficial layer of the dermis or epidermis. The sections through the ocellus do not show any obvious differences in thickness or arrangement of skin structures as compared with the normal pigmented areas.

It should be noted especially that no nerve fibers or specialized nerve endings were recognized in the dermis of either the ocellar or the pigmented regions of the skin, although distinct nerve fibers could be seen in the subcutaneous tissue and in the underlying muscle bundles. It should be noted further that no extensive or unusual vascular arrangement occurs in the region of the ocellus.

THE HISTOCHEMISTRY OF THE SECTION

Histochemically, the epidermis shows nothing striking. Its surface gives a moderate reaction for sulfhydryl groups and an intense reaction for disulfide linkages, as would be expected if its

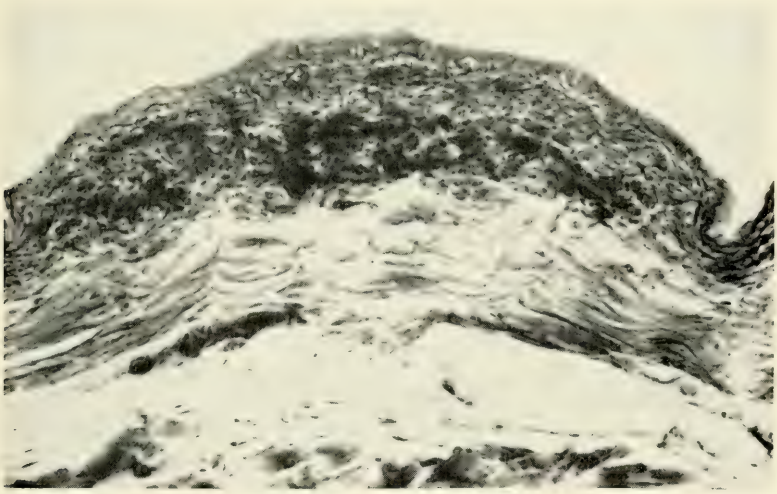

Fig. 4. Cross-section through the same ocellus as shown in Figures 2, 3. Note the intense PAS-positive reaction of the superficial layer of the dermis. Periodic-acid-Schiff reaction counterstained with hematoxylin 400X.

scales were keratinized. *The epidermis covering the white spot is identical with that covering pigmented dermis. The deep layer of the dermis also seems to be identical* below the white and pigmented skin. The reactions of both collagenous and elastic tissue present nothing novel. The superficial dermis of the white spot is of special interest, however. In hematoxylin and eosin preparations, it is much more lightly stained than the deep portion of the dermis, contains less collagen and is far more cellular. However, the cytoplasmic limits (and the cell boundaries) of these cells cannot be made out. The impression, therefore, is of tenuous, presumably branched cytoplasmic processes.

Histochemically, this superficial region of the dermis (the cell cytoplasm?) shows a number of characteristics. Thus it gives an intense positive PAS reaction which is diastase resistant (Fig. 4). Further, it shows a moderately strong reaction for sulfhydryl groups which is not greatly intensified with the disulfide test. With controlled pH staining it shows only a weak staining with light green even at low pH's, but a moderate (pH 5) to heavy (pH 8) staining with methylene blue or thionine. From these results it seems possible to conclude that the cells of this region are not vacuolated (as might appear from H and E sections), but contain a substance or substances not readily stained by routine methods. The results of the PAS method show that this material contains numerous 1-2 glycol linkages, but is not glycogen. The results of the sulphydryl and the controlled pH methods indicate a moderately basophilic protein which contains appreciable cystine or cysteine or both. A complete absence of staining with Sudan black B indicates that it is not a phospholipid, a glycolipid, or a lipoprotein. Thus these findings suggest the presence of a mucoprotein or mucopolysaccharide. A heavy accumulation of connective tissue ground substance would account for these observations except for the absence of metachromasia. While the fixation in this instance is not optimum for a critical evaluation, the appearance of the sections favors an intra- rather than extracellular localization.

Furthermore, upon the examination of unstained sections, the region shows no marked granulation under either the light or phase-contrast microscope. The reflecting pigment guanine is supposedly insoluble in all of the reagents used for fixation and embedding. Guanine crystals, if present, should therefore be evident in unstained sections, and their absence rules out this pigment as the source of the white appearance.

DISCUSSION AND CONCLUSIONS

Basically there are no important differences between the present more extensive histological description and that originally furnished by Parker (1939, p. 658). He accented the differences between the tissue underlying the glistening white spot and that below the remainder of the dermis. The points emphasized were five: (1) a reduction of the epidermis to one-half its normal thickness, (2) absence of the chromatophore layer, (3) presence of a mass of spongy mesenchymatous tissue, (4) large intra- or intercellular spaces in the spongy tissue, and (5) absence of nerve endings. Parker emphasized the poor preservation of the material. Neither the stains nor the method of preservation were specified, but the photomicrographs suggest that only H and E or a similar routine staining technique was employed.

We differ in failing to find either vacuolated spaces in the spongy tissue or a reduction in thickness of the overlying epidermis. It seems clear that the presence of "vacuolated spaces" could be accounted for entirely by the fact that Parker's material was poorly preserved for histological purposes and that these are presumably fixation or shrinkage artifacts. With regard to the variation in thickness of the epidermis, Parker's photographs indicate that such a reduction does not coincide with the absence of melanin. Our sections indicate similar and regional differences in the thickness of the epidermis of some of the pigmented scales.

On the basis of the additional evidence reported in this paper, the following statements may be made:

Sanderson's observations and Parker's comments thereon contain a number of inconsistencies. Sanderson reported that the light is (1) under the control of the animal and can be turned on and off, (2) much brighter the first time it is used after a period of quiescence, and (3) brightest just *after* the spot has been subjected to illumination. In spite of this Parker suggested that the organs are reflectors rather than truly luminous. A reflector might be capable of producing the first of the three effects, but the last two would be characteristic of true luminescence.

None of the subsequent field observers has reported similar results. Their experiments cover more specimens and a longer period than does Sanderson's report. However, in all but one case the species involved are different, though externally very similar and probably closely related to the form on which the original report had been based.

The lateral ocelli of *Proctoporus* might represent one of four types of structures: independent light-generating organs (either innervated or under hormonal control), receptacles for light-generating organisms, specialized reflecting structures, or simply nonpigmented "white" spots with a black margin.

The first of these possibilities is made unlikely by a number of factors. The center of the ocellus shows no gross difference from the surrounding skin and can be recognized only by the absence of melanin. The ocellus does not, in any manner, resemble previously described luminescent organs. The cells of the white spot do not have an epithelioid appearance and in no way resemble cells previously described for luminescent organs. There is neither special innervation nor vascularization. This is particularly important since Sanderson indicated that the light was turned on quite rapidly.

The absence of any vacuoles or staining reactions characteristic of bacteria seems to rule out the possibility of storage of luminous microorganisms.

There are certain difficulties in distinguishing between reflecting structures and plain white spots. It seems certain that the white spots do not represent one of the more complicated reflecting systems since specialized epidermal cells and similar structures are lacking.

It is, therefore, concluded that the white appearance is produced by an inter- or intracellular substance, which lies at the same level of the skin as the dermal melanophores, and which may or may not have special reflecting properties. The further possibility exists that a local accumulation of connective tissue ground substance, or a specific intracellular mucoprotein or mucopolysaccharide could be strongly reflective.

This conclusion is in good agreement with all reports of observations on live animals but Sanderson's. If any of the species of *Proctoporus* or related teiids are luminescent, they would seem to glow only under very special circumstances and by a yet undescribed mechanism. However, the inconsistencies of the initial reports by Sanderson and Parker and the completely negative result of the investigations presented here force us to reject, for the present, any interpretation of these "portholes" as bioluminescent organs.

Our findings, furthermore, suggest a quite different and interesting possibility. The location and appearance of the protein-containing cells in the superficial dermis suggests that they could be potential melanophores which have formed no pigment.

Clearly, proof of this would involve a study of the histochemistry of such "prepigmented" melanophores. Nevertheless, it seems possible to speculate that this color pattern in lizards might be achieved through a precise local control of the chemistry of the melanophore cells and hence, might prove an interesting area for the study of specified control of cellular differentiation.

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MID-SCYTHIAN AMMONITES FROM IWAI FORMATION, JAPAN

BY BERNHARD KUMMEL and SUMIO SAKAGAMI

Lower Triassic ammonoids are known from only a few localities in Japan. The first fair-sized fauna to be recorded was that from the Taho formation on the island of Shikoku described by Yehara (1928). The majority of ammonite species from the Taho formation belong in *Anasibirites* and *Hemiprionites;* Yehara had erroneously assigned these ammonites to species of *Meekoceras, Kymatites, Ophiceras,* and *Xenodiscus.* This fauna is clearly representative of the zone of *Anasibirites multiformis,* which is known from Timor, Kashmir, the provinces of Kiangsu and Hupeh in China, British Columbia, Queen Elizabeth Islands, and western United States.

A most important contribution to our knowledge of the Lower Triassic of Japan was made by Sumio Sakagami who in 1955, described a small fauna of ammonites from the Iwai formation, Kaizawa Valley, Hinode-mura, Nishitama-gun, Tokyo-to. Sakagami had specimens from two fossiliferous beds, seventeen meters apart. The lower fauna was concluded to be of early Scythian age and the upper fauna to be mid-Scythian (*Meekoceras* zone) in age.

Correspondence between the authors about this fauna and the study of additional material bear out the conclusion that the faunas of both fossiliferous beds are of *Meekoceras* zone age. The object of this paper is to further document the species present and the age of the Iwai formation.

The Iwai formation is well exposed in the Kaizawa Valley where Sakagami has recognized four members. In ascending order these members are: (a) more than 40 m. of black and bluish sandstone, (b) 10 m. of shale, (c) 10 m. of sandstone, and

finally (d) about 25 m. of black shale which contains the two fossiliferous units. The lower fossil bed occurs about 2 meters above the base of the upper member, where the fossils occur in lenses of black limestone. The species identified from this horizon are:

Dieneroceras iwaiense (Sakagami)
Dieneroceras sp. indet.
Owenites shimizui (Sakagami)
Paranannites sp. indet.
Aspenites sp. indet.
Juvenites sp. indet.

The upper fossil bed lies about 17 meters above the lower fossil bed and consists of marl lenses from which Sakagami obtained a single specimen that has been assigned to *Aspenites*.

The genera and species in both the lower and upper beds are forms very characteristic of the mid-Scythian *Meekoceras* zone. Faunas of this age are well known from several localities in California, Nevada, Utah, and Idaho (Smith, 1932; Kummel, 1954); from the Queen Elizabeth Islands of Arctic Canada (Tozer, 1958); from the Island of Timor (Welter, 1922); from Southland, New Zealand (Kummel, 1959); from the northern Caucasus Mountains, Russia (Kiparisova, 1958); and finally faunas of this age appear to be represented in the Kolyma River region of northeastern Siberia (Popov, 1939) and in Yugoslavia (Petković and Mihajlović, 1935).

Of all the forms represented in the Iwai faunas the single specimen of *Owenites* furnishes the best clue as to their age. *Owenites shimizui* (Sakagami) is an immature form that, however, compares very closely with *Owenites koeneni* from the *Meekoceras* beds of western United States. *Owenites* is also known from Timor, New Zealand, and the northern Caucasus Mountains, Russia. *Dieneroceras* is a longer ranging genus but *Dieneroceras iwaiense* (Sakagami) is close in its general conch morphology to *D. dieneri* from the *Meekoceras* beds of the western United States. The Iwai specimens placed in *Dieneroceras* sp. indet. are more involute than *D. iwaiense* and of very different appearance. These specimens lack any sign of a suture and the identification can only be considered as tentative. *Juvenites* is another genus of widespread occurrence in the *Meekoceras* zone of western United States but it does range above and below this zone. The single specimen from the upper fossiliferous bed which Sakagami identified as *Aspenites* sp. was not available for study.

The specimen is fragmentary but appears from the illustration to be reasonably placed in *Aspenites*. Another specimen has been uncovered from the lower fossiliferous bed that is of much better preservation and is without any doubt an indeterminate species of *Aspenites*.

Previous assessments of the age of the Iwai formation rested largely on the identification of the most common species in the lower fauna — *Dieneroceras iwaiense* (Sakagami) – as an *Ophiceras*. Shimizu (1932) appears to have been the first to comment on the Iwai ammonites, though Fujimoto (1926) discussed some

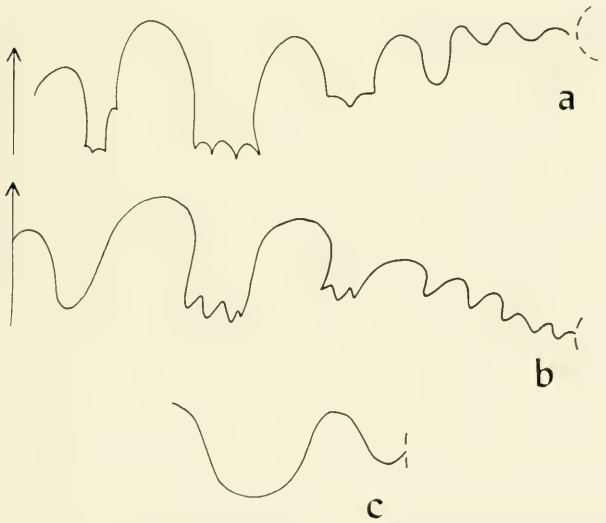

Fig. 1. Diagrammatic representation of the suture of (a) *Owenites shimizui* (Sakagami), holotype (from Sakagami, 1955, pl. 2, fig. 2c) X 7; (b) *Owenites koeneni* Hyatt and Smith, from a paratype of 15 mm. in diameter (from Hyatt and Smith, 1905, pl. 10, fig. 10), X 8; (c) *Dieneroceras iwaiense* (Sakagami), partial suture of holotype (from Sakagami, 1955, pl. 1, fig. 1c), X 10.

Pseudomonotis, earlier. Forms like *Dieneroceras iwaiense* are extremely difficult to place stratigraphically, and it was not until the presence of such genera as *Owenites* and *Aspenites* was established that both the age and generic assignment of the "*Ophiceras*" could be properly evaluated.

SYSTEMATIC DESCRIPTIONS

Family DIENEROCERATIDAE Kummel, 1952

Genus DIENEROCERAS Spath, 1934

DIENEROCERAS IWAIENSE (Sakagami)

Plate 1, figures 3-5; Plate 2, figures 7-9

Ophiceras iwaiense Sakagami, 1955, pp. 135-136, pl. 1, figs. 1-9.
Ophiceras sp. Sakagami, 1955, pp. 136-137, pl. 1, figs. 10-11.
Dieneroceras iwaiense, Kummel, 1959, p. 430.

The dominant element in the lower ammonoid bed at Iwai is a new species of *Dieneroceras*. Sakagami (1955) had eleven specimens that he described and illustrated, and there are now four additional specimens in the collections of the Museum of Comparative Zoology. The conch is very evolute, each whorl embracing the preceding one only slightly. The whorls are compressed with broadly arched flanks which converge slightly toward the venter. The ventral shoulder is subangular and distinctly marked and the venter is a low broad arch. The umbilical shoulders are broadly rounded. The serpenticone coiling of the conch exposes all of the inner whorls which are more rounded (and less compressed) than the outer volutions. The conch is smooth, except that on some of the specimens there appear to be extremely faint radial folds. The measurements of the better preserved specimens are as follows:

	D	H	W	U
		(Measurements in mm.)		
*MCZ 5282a (Topotype)	22.5	7.7	5.3	11.0?
TUE 5255 (Paratype)	21.0	15.8	—	10.1
TUE 5254 (Paratype)	20.7	7.0	—	10.6
TUE 5252 (Paratype)	20.5	6.5	—	9.0
TUE 5257 (Paratype)	18.0	6.2	—	8.7
TUE 5251 (Holotype)	15.5	4.5	3.7	7.5
MCZ 5282b (Topotype)	15.0?	4.5	—	7.7
TUE 5256 (Paratype)	15.0	5.0	—	7.2
TUE 5253 (Paratype)	9.4	3.0	—	4.5

The suture is faintly and only partially visible on the holotype and on one of the paratypes and consists of a large first lateral lobe, and a much smaller second lateral lobe on the umbilical wall. It is not possible to determine whether or not the lobes are denticulated.

*MCZ = Museum of Comparative Zoology; TUE = Tokyo University of Education

Remarks. Many of the mid- and late Scythian ammonoids, that have on various occasions been assigned to *Ophiceras*, are now commonly placed in *Dieneroceras* which is interpreted as a persisting generalized stock out of the early Scythian ophiceratids (Spath, 1934, p. 124; Kummel, 1952, p. 849, 852). In the *Meekoceras* fauna of western United States, *Dieneroceras* is represented by *D. dieneri* (Hyatt and Smith), *D. knechti* (Hyatt and Smith), *D. subquadratum* (Smith), and some as yet undescribed species. The specimens assigned by Smith (1932, p. 50, pl. 54, figs. 1-17; plate 56, figs. 13-18) to *Ophiceras sakuntala* Diener are also a species of *Dieneroceras*. As now interpreted the species assigned to *Dieneroceras* show a wide range in morphological features, especially marked in the cross-section of the whorls.

Dieneroceras iwaiense is morphologically most similar to the genotype, *D. dieneri*. This is especially noticeable in the angular ventral shoulders and low arched venter. The illustrations of the holotype and paratype of *D. dieneri* originally described by Hyatt and Smith (1905, pl. 8, figs. 16, 17, 19, 20) are inaccurate drawings; these types are re-illustrated here on Plate 3, figures 1-4. The Japanese species, however, is more compressed and the whorls converge toward the ventral region more than in *D. dieneri*. The genotype bears faint strigations which are most often not preserved, as already noted by Smith (1932, p. 49). None of the Japanese specimens show any trace of strigations.

Occurrence. Lower fossiliferous bed of upper member of Iwai formation, Kaizawa Valley, Iwai, Hinode-mura, Nishitama-gun, Tokyo-to, Japan.

Repository. MCZ 5282a,b,c, (Pl. 1, figs. 3-5); TUE 5254, paratype (Pl. 2, fig. 7); TUE 5251, holotype (Pl. 2, figs. 8, 9).

Dieneroceras sp. indet.

Plate 1, figure 1; Plate 2, figure 10.

Vishnuites sp. Sakagami, 1955, p. 137, pl. 1, fig. 12.

In the original collection described by Sakagami (1955), he had a single, small, incomplete specimen of which only one side of a half of a volution was preserved (Pl. 2, fig. 10 of this report). Four additional, though fragmentary, specimens are now available. The best specimens are illustrated on Plate 1, figure 1. The conch is small, compressed, and involute; the whorl flanks are broadly arched merging with a well rounded umbilical

shoulder on the one side, but the ventral shoulders are subangular. The venter is broadly arched. The whorl sides bear weak, slightly sinuous, narrow folds which are most pronounced on the dorsal half of the whorl side. Unfortunately, no suture is preserved on any of the specimens.

Remarks. The incompleteness of the specimens and the absence of any sutures makes identification of forms like this extremely uncertain. The specimens could very possibly be juveniles of larger forms. Under these circumstances the assignment to *Dieneroceras* can only be considered as tentative but the most reasonable conclusion for the moment.

Occurrence. Lower fossiliferous bed of upper member of Iwai formation, Kaizawa Valley, Iwai, Hinode-mura, Nishitama-gun, Tokyo-to, Japan.

Repository. MCZ 5283 (Pl. 1, fig. 1); MCZ 5286 (unfigured specimens); TUE 5260 (Pl. 2, fig. 10).

Family PROPTYCHITIDAE Waagen, 1895
Subfamily OWENITINAE Spath, 1934
Genus OWENITES Hyatt and Smith, 1905

OWENITES SHIMIZUI (Sakagami)
Plate 2, figures 5, 6

Kingites shimizui Sakagami, 1955, pp. 138-139, pl. 2, figs. 2a c.
Owenites shimizui (Sakagami), Kummel, 1959, p. 430.

The holotype and only specimen of this species is a small, juvenile specimen that can with confidence be assigned to *Owenites*. The specimen measures 21.0 mm. in diameter, 11.3 mm. for the height of the last whorl, 8.0 mm. for the width of the last whorl, and the umbilicus is 1.5 mm. in diameter. The conch is involute with broadly arched whorl sides that converge, forming a sharp acute venter. The only ornamentation consists of radial growth lines.

The suture (Fig. 1a) is ceratitic and typical of that found in species of *Owenites*. It consists of a narrow, denticulated ventral lobe, a large denticulated first lateral lobe, a smaller second lateral lobe and a series of small auxiliary lobes. This suture is almost identical in its basic plan to that of a specimen of 15 mm. in diameter of *Owenites koeneni* Hyatt and Smith (1905, pl. 10, fig. 10) reproduced here on Figure 1b.

Remarks. Mature specimens of *Owenites* show marked excentrumbilication on the outer whorls producing a deep funnel-shaped umbilicus. The immature volutions (roughly up to 25-30

mm.) form a tightly involute conch and the small umbilicus shows no tendency toward excentrumbilication. *Owenites shimizui* is almost identical in conch shape and proportions to specimens of comparable size of *O. koeneni* of the *Meekoceras* zone of western United States. A paratype of *O. koeneni* originally illustrated by Hyatt and Smith (1905, pl. 10, figs. 7-9) by a poor drawing is illustrated here on Plate 3, figures 5-7. This specimen measures 15 mm. in diameter and is the specimen from which the suture of Text-figure 1b was obtained. The suture is very similar in these two species at about the same diameter, differing only in minor details. The resemblance to *Kingites* in conch shape and suture is more apparent than real.

Owenites is one of the best mid-Scythian zonal markers in the Circum-Pacific region. In western United States (California, Nevada, Utah, and Idaho) the genus is very common in the zone of *Meekoceras gracilitatus*. The genus was first established for specimens from the *Meekoceras* limestone in the Inyo range, California (Hyatt and Smith, 1905, p. 82). Smith (1932) recognized a number of additional species of *Owenites* in western United States but most of these appear to be merely intraspecific variants of *O. koeneni*.

The Timor *Owenites egrediens* Welter (1922) has a narrow, rounded keel-like venter formed by the shell, but the internal cast has a sharp venter. Likewise the Timor species is generally more inflated, producing a broader and deeper umbilical funnel. The suture also differs slightly in the shape of the lobes and the auxiliary series. Recently, a specimen of *Owenites* cf. *koeneni* Hyatt and Smith, has been described from beds of Pre-Etalian age in western Southland, New Zealand (Kummel, 1959). Outside of the Circum-Pacific region, *Owenites* has been recorded only from the northern Caucasus Mountains.

Occurrence. Lower fossiliferous bed of upper member of Iwai formation, Kaizawa Valley, Iwai, Hinode-mura, Nishitama-gun, Tokyo-to, Japan.

Repository. TUE 5262, holotype (Pl. 2, figs. 5, 6).

Family PARANANNITIDAE Spath, 1930
Subfamily PARANANNITINAE Spath, 1930
Genus PARANANNITES Hyatt and Smith, 1905

PARANANNITES sp. indet.
Plate 2, figures 1, 2

Proptychites aff. *rosenkrantzi* Spath. Sakagami, 1955, pp. 137-138, pl. 2, figs. 1a, b.

Paranannites sp. indet., Kummel, 1959, p. 430.

This form is represented by a single specimen of only moderate preservation. The conch is involute, compressed, with flattened, parallel whorl sides and a broadly rounded venter. It measures 33.1 mm. in diameter, 15.3 mm. for the height of the last whorl, 9.3 mm. for the width of the last whorl, and 6.5 mm. for the diameter of the umbilicus. Unfortunately no suture is preserved.

Lower Triassic ammonoids of this conch morphology are difficult to identify, and without the suture generally impossible to recognize. The fact that the associated fauna includes species of *Owenites* and *Juvenites* precludes the probability that this specimen could represent a species of *Proptychites*, which is generally an earlier Scythian form. The associated genera indicate a mid-Scythian age for the fauna and, of the ammonites of this age, *Paranannites* comes the closest in its conch morphology to this specimen from Iwai, Japan. *Paranannites aspenensis* from the *Meekoceras* zone of western United States has a conch of the same degree of involution and rounded venter which, however, is more inflated—the whorl width being just slightly less than the whorl height. *Paranannites pertenuis* Smith (1932, p. 99, pl. 31, figs. 13-15) has a laterally compressed conch with flattened sides like the Iwai specimen (Pl. 3, figs. 9, 10). This species of Smith is believed to be a synonym of *P. aspenenesis*. The tentative placement of this specimen in *Paranannites* is, of course, based on the assumption that it is a mature specimen. If, however, it is a juvenile form it is most likely not a *Paranannites*, and then could possibly be the inner whorls of a *Flemingites* or *Arctoceras*, or other such larger ammonoids of mid-Scythian age.

Occurrence. Lower fossiliferous bed of upper member of Iwai formation, Kaizawa Valley, Iwai, Hinode-mura, Nishitama-gun, Tokyo-to, Japan.

Repository: TUE 5261 (Pl. 2, figs. 1, 2).

Genus JUVENITES Smith, 1927

JUVENITES sp. indet.
Plate 1, figure 2

The collection contains a single specimen in which only one side of a half volution is preserved. The specimen measures approximately 16.4 mm. in diameter, 7.3 mm. for the height of the last whorl, and the umbilicus is 5.0 mm. in diameter. The conch is involute with broad, depressed whorls and a broadly rounded

venter that grades imperceptibly onto the lateral areas. The conch bears very conspicuous forward projecting constrictions. There appear to be six such constrictions on the half volution. No indication of a suture is preserved.

Remarks. The lack of a suture and the incompleteness of the specimen necessarily make the present identification tentative. Even so, in consideration of the association with *Owenites* and *Aspenites* which are clearly mid-Scythian in age, the assignment of this specimen to *Juvenites* appears reasonable. The constrictions on the Iwai specimen are similar in depth and distinctness to those in *Juvenites septentrionalis* Smith (1932, pl. 31, figs. 31-32) but in the latter species the constrictions are radial. Strongly projected constrictions somewhat similar to those on the Iwai specimen are present on *Juvenites thermarum* (Smith, 1932, pl. 21, figs. 11-12, 16-17, 19-20).

Occurrence. Lower fossiliferous bed of upper member of Iwai formation, Kaizawa Valley, Iwai, Hinode-mura, Nishitama-gun, Tokyo-to, Japan.

Repository. MCZ 5284 (Pl. 1, fig. 2).

Family HEDENSTROEMIIDAE Waagen, 1895
Subfamily ASPENITINAE Spath, 1934
Genus ASPENITES Hyatt and Smith, 1905

ASPENITES sp. indet.
Plate 2, figures 3, 4; Plate 3, figure 8

Aspenites sp. Sakagami, 1955, p. 139, pl. 2, figs. 3a, b.

One of the authors (Kummel) has not had the opportunity to examine the single representative in the collection originally described by Sakagami (1955, p. 139) who states that it agrees with *Aspenites* of the western United States but the suture is not preserved. As well as one can tell from the illustration, this identification appears to be reasonably correct. Another specimen has since been uncovered from the lower ammonite bed that appears without doubt to be a juvenile representative of *Aspenites*. This specimen (MCZ 5285) measures only 8.0 mm. in diameter and is a completely involute conch, greatly compressed, with broad arched flanks which converge to a narrow, keeled venter (Pl. 3, fig. 8). No suture is preserved. The specimen is almost identical with specimens of comparable size of *Aspenites acutus* Hyatt and Smith (Smith, 1932, pl. 30, figs. 6-7, 9, 11-12).

Aspenites is fairly abundant in the *Meekoceras* beds of western United States and in Timor.

Occurrence. Both upper and lower fossiliferous beds of upper member of Iwai formation, Kaizawa Valley Iwai, Hinode-mura, Nishitama-gun, Tokyo-to, Japan.

Repository. TUE 5263 (Pl. 2, figs. 3, 4); MCZ 5285 (Pl. 3, fig. 8).

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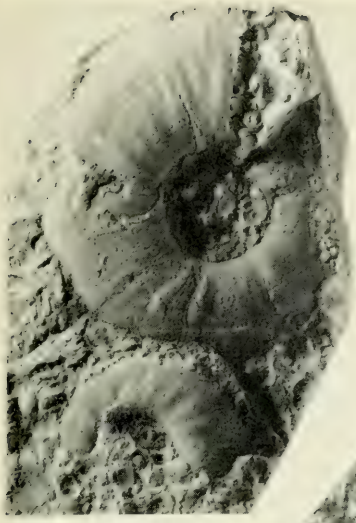
EXPLANATION OF PLATE I

The specimens illustrated on this plate are from the lower fossiliferous bed of the Iwai formation, Kaizawa Valley, Hinode-mura, Nishitama-gun, Tokyo-to, Japan, and are preserved in the Museum of Comparative Zoology.

Fig. 1. *Dicneroceras* sp. indet., MCZ 5283, X 2.

Fig. 2. *Juvenites* sp. indet., MCZ 5284, X 3.

Figs. 3-5. *Dicneroceras iwaiense* (Sakagami), topotypes, MCZ 5282a,b,c, X 3.



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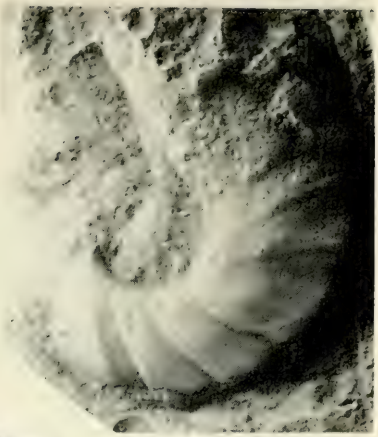

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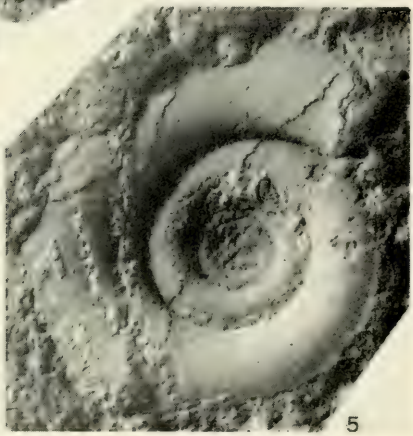

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PLATE 1

EXPLANATION OF PLATE 2

The specimens illustrated on this plate are from the Iwai formation, Kaizawa Valley, Iwai, Hinode-mura, Nishitama-gun, Tokyo-to and are preserved in the collections of the Geological and Mineralogical Institute, Tokyo University of Education.

Figs. 1, 2. *Paranannites* sp. indet., from lower fossiliferous bed of Iwai formation, TUE 5261, X 2.

Figs. 3, 4. *Aspenites* sp. indet., from upper fossiliferous bed of Iwai formation, TUE 5263, X 1.

Figs. 5, 6. *Owenites shimizui* (Sakagami) from lower fossiliferous bed of Iwai formation, TUE 5262, X 2.

Figs. 7-9. *Dieneroceras iwaiense* (Sakagami) from lower fossiliferous bed of Iwai formation. Fig. 7, paratype, TUE 5254, X 2; figs. 8, 9, holotype, TUE 5251, X 2.

Fig. 10. *Dieneroceras* sp. indet. from lower fossiliferous bed of Iwai formation, TUE 5260, X 2.

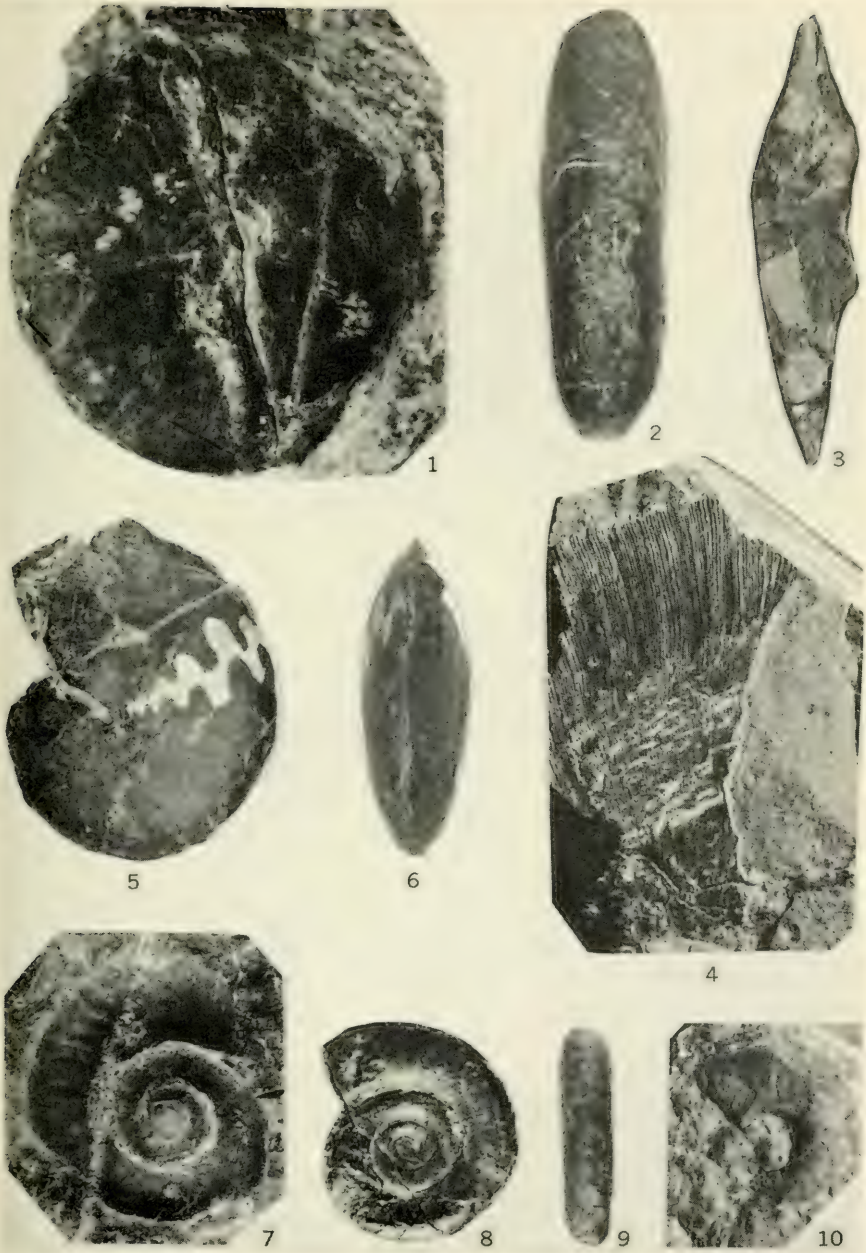

PLATE 2

EXPLANATION OF PLATE 3

Figs. 1-4. *Dieneroceras dieneri* (Hyatt and Smith), from *Meekoceras* beds in Wood Canyon, 9 miles east of Soda Springs, Aspen Ridge, Idaho. Figs. 1, 2, holotype, USNM 75260, X 1.5; 3, 4, paratype USNM 75260a, X 2.

Figs. 5-7. *Owenites koeneni* Hyatt and Smith, from *Meekoceras* beds, Union Wash, Inyo Range, Inyo County, California. Paratype USNM 75261b, X 2.

Fig. 8. *Aspenites* sp. indet. from lower fossiliferous bed of Iwai formation, Kaizawa Valley, Iwai, Hinode-mura, Nishitama-gun, Tokyo-to, Japan, MCZ 5285, X 4.

Figs. 9-10. *Paranannites pertenuis* Smith, from *Meekoceras* beds in Wood Canyon, 9 miles east of Soda Springs, Aspen Ridge, Idaho. Holotype, USNM 74960, X 1.5.

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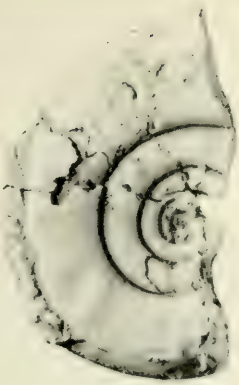

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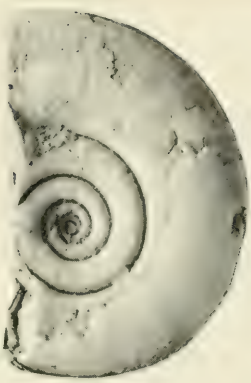

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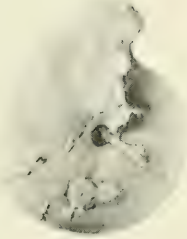

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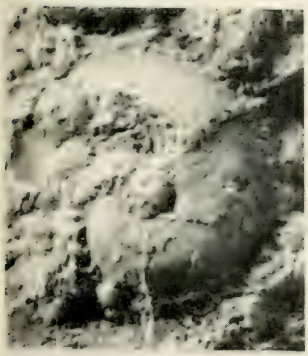

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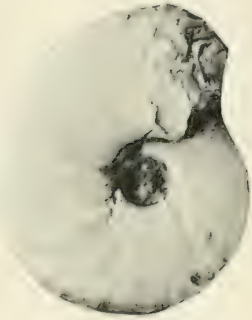

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PLATE 3

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. DECEMBER 19, 1960 NUMBER 127

NOTES ON THE CRANIAL ANATOMY OF NECROLEMUR

By

E. L. SIMONS [1] AND D. E. RUSSELL [2]

INTRODUCTION

The large number of well-preserved skulls of *Necrolemur antiquus* of the late Eocene Quercy phosphorites of south central France allow for much more detailed study of cranial anatomy in this primate than is possible for most early members of the order. In spite of the fact that cranial osteology can be studied in great detail, views as to the taxonomic position of this primate, and of the allied genera *Microchoerus*, *Nannopithex*, and *Pseudoloris* show considerable variance.

Although not all of the same provenance, little dental variability is evidenced in specimens of *Necrolemur antiquus* examined by us. In the course of this study, however, a number of differences in position and size of basicranial foramina have been observed, which are in line with mutability of cranial foramina (in individuals of the same species) reported by other authors (see Edinger and Kitts, 1954). Also, in *Necrolemur* the probability remains that known specimens differ considerably in age (from early Bartonian to late Ludian provincial ages, at least), but locality data are inadequate for precise age determinations. Comparison of upper dentitions in the M.C.Z. and Paris skulls has failed to show any dental basis for species distinctions among them.

To date, the most detailed studies of the cranium of *Necrolemur* have been by Stehlin (1916) and by Hürzeler (1948). Stehlin's thorough and excellent description can scarcely be improved on.

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but copies of this work are not as generally available as could be wished. Also, the implications of some of his early observations seem to have been neglected in later literature. In some rather significant points, recent examination of more and different skulls permits comments supplementary to his work.

ACKNOWLEDGEMENTS

The authors would like to take this opportunity to thank Drs. J.-P. Lehman, Curator of Fossil Vertebrates at the Muséum National d'Histoire Naturelle in Paris, and A. S. Romer of the Museum of Comparative Zoology at Harvard for generously giving permission to publish on the specimens in their respective charges. Preparation of the figures, by Miss Ellen Cole, was supported by a grant from the Wenner-Gren Foundation for Anthropological Research.

ABBREVIATIONS

In the absence of specimen numbers, the Paris Museum skulls of *Necrolemur* have been numbered 1 through 5 for convenience of reference. Abbreviations used in this paper are as follows: M.C.Z., Museum of Comparative Zoology at Harvard College. Montauban, Natural History Museum (Geological Collection), Montauban, France. Paris, National Museum of Natural History, Paris.

CRANIAL CHARACTERS

I. AUDITORY REGION

Most of the information, published to date, regarding the components of the auditory bulla in *Necrolemur* comes from Montauban 9, which has been discussed by both Stehlin and Hürzeler. Even though this skull was prepared with considerable skill, the crystalline calcite filling was apparently confused with the very similar appearing bone in the region of the epitympanic recess. Consequently, the route of the stapedial artery across the tympanic cavity of the middle ear was lost just anterior to the fenestra ovalis. The extrapetrous portion of the Fallopian aqueduct was lost as well. Preparation of Paris 2 has revealed more details of the epitympanic region (Fig. 1).

Exposure of the inside of the bulla in Paris 2 and 5 indicated primarily the lack of a free annular tympanic ring. Moreover, studies by Simons (in press) on a specimen of *Necrolemur* at the

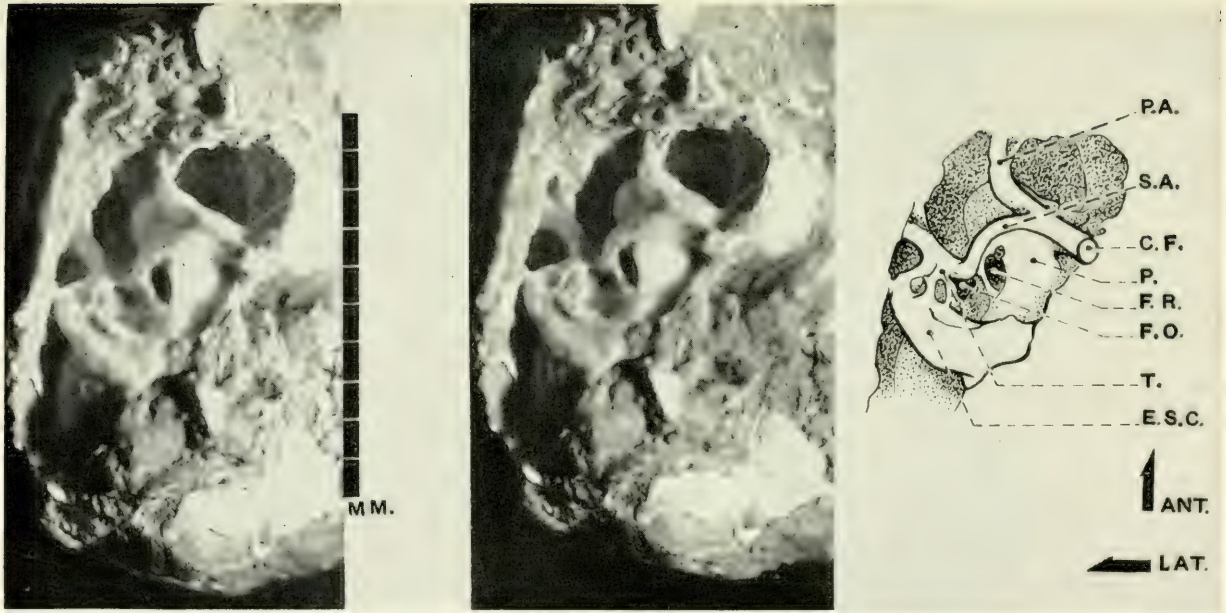

FIGURE 1

Necrolemur antiquus, Paris 2, interior of right bulla. x 5. Stereoscopic depth exaggerated.
Abbreviations: *P.A.*, promontory artery; *S.A.*, stapedial artery; *C.F.*, carotid foramen; *P.*, promontorium; *F.R.*, fenestra rotunda; *F.O.*, fenestra ovalis; *T.*, "T" of extrapetrous portion of Fallopian aqueduct; *E.S.C.*, external semicircular canal.

British Museum (Natural History) demonstrate that the ectotympanic element is tubular, and medially fused to the ventral bulla wall. Hürzeler's evidence (1946:353; 1948:28) of the presence of a free ring, therefore, can no longer be accepted. The bone he identified as such had to be removed during preparation to expose the carotid canal and thus cannot be re-examined. In M.C.Z. 8879 the meatal tubes are reasonably well preserved but one of the Paris skulls shows an even more complete osseous meatus. Together, these indicate that the ectotympanic (external to the bulla) is about as long as the transverse diameter of the foramen magnum, curves slightly backward, and may be broadest at the external aperture. None of the fossil or recent Lemuroidea have this sort of meatus.

Hürzeler (1948:27) cites M.C.Z. 8879 as not showing any evidence of a fused tympanic ring. Nevertheless, four and possibly more transverse struts are exposed on the ventrolateral face of the right bulla of the Harvard skull. These bars are supports for the internal rim of the tubular ectotympanic.

Also of interest is the fact that the anterior route of the promontory artery (true entocarotid) is apparently variable. In Montauban 9, it curves sharply anteromedially shortly after leaving the promontory of the petrosal. In Paris 2, this curving is much less accentuated. Some crushing is to be allowed for in the tympanic region of the latter specimen but the amount of curvature illustrated by Hürzeler (1948, figs. 30 and 31) for Montauban 9 is not indicated in the Paris skull. It should be further noted that this bony tube does not lie in a horizontal plane in Montauban 9 and Paris 2, but slopes anterodorsally at an angle of about 45°.

The stapedial artery, like the promontory artery, remained enclosed in a bony tube throughout its route within the bulla. Branching from the promontory artery just inside the carotid foramen, the stapedial artery curved dorsally, lying on and following the form of the petrosal promontory. It then passed anterior to the fenestra rotunda to the bottom of the fenestra ovalis. There it diverged laterally, crossing the fenestra ovalis, and continued anteriorly nearly parallel to the promontory artery (Fig. 1). The groove mentioned by Hürzeler (1948:31) is surely a remnant of the stapedial tube, as he suggested. The exit of the stapedial artery appears to be at the dorsoanterior base of the external auditory meatus.

The extrapetrous portion of the Fallopian aqueduct is also enclosed up to, or nearly up to, its exit at the stylomastoid foramen. Its route lies lateral to the fenestra ovalis, just above the stapedial artery and continues posteriorly under the external semicircular canal. At this point, the tube forms a "T" giving rise to the small anterolateral opening and a larger posteromedian branch. The former is a natural foramen. Damage to the latter region makes it impossible to say whether or not the more posterior branch continued as an enclosed tube to the stylomastoid foramen. In Paris 2, this foramen is single, in Paris 1, double. Without exposing the interior of the bulla in Paris 1 a possible connection between the branching Fallopian aqueduct and the double stylomastoid opening cannot be confirmed. That the anterolateral foramen of the "T" in Paris 2 could have given passage to the chorda tympani seems likely.

Regarding the foramen designated FX, "Foramen von unbekannter Bedeutung," by Hürzeler (1948:fig. 28), it seems probable that this represents the opening of the inferior petrous sinus, as originally stated by Stehlin (1916:1355).

Contrary to the views of a few students, we find little distinction between *Tarsius* and *Necrolemur* in the major carotid relationships, both inside and outside the bulla. The two genera appear to agree in those features of the carotid circulation which distinguish tarsiers from Malagasy lemurs, adapids and lorises (see Le Gros Clark, 1959:151). Location of the internal carotid foramen in *Tarsius* on the ventral surface of the bulla (instead of on the median wall) constitutes a slight difference from *Necrolemur*, but it should be stressed that placement of this foramen in the fossil species does approximate the situation in *Tarsius*, being more ventral than in most, if not all, other prosimians. Furthermore, *Necrolemur* and *Tarsius* are alike in having both stapedial and promontory branches within the bulla, encased in bony canals or tubes, with the promontory division the larger. In typical Lemuriformes (Malagasy lemurs, adapines and notharctines), the carotid foramen has a quite different location at the posteroexternal angle of the bulla and, inside it, the promontory division is very small (Gregory, 1920:174-180). Lorises and the cheirogaleine lemurs differ also, in that the carotid divides outside the entotympanic and the main branch enters the skull through the foramen lacerum medium instead of going through the bulla. A middle lacerate foramen is not present in *Tarsius* and *Necrolemur*. The few differences between these two genera to be observed in the auditory region

seem best understood with reference to the effects of the anterior shifting of the foramen magnum and greater inflation of the anterointernal part of the bulla in *Tarsius*. Some primitive features are also to be seen in the Eocene form. For instance, the canal for the promontory artery in *Necrolemur* is only slightly thicker than that for the stapedial. In *Tarsius* this difference is more pronounced. What is of general significance is that when *Necrolemur* differs from *Tarsius* it is usually intermediate between the latter and yet more primitive prosimians. One could hardly expect an Eocene tarsioid to be otherwise.

II. BASICRANIUM

Stehlin (1916:1351) mentioned that the alisphenoids participated in the composition of the anterior wall of the bulla. However, Hürzeler (1948:26) has pointed out that, although the bulla is overlapped by the alisphenoids, this does not permit the definite statement that the alisphenoids constitute a part of the true bulla wall. In Montauban 9, it is possible to follow the suture between the bulla and its neighboring elements from the carotid foramen around the anterior end to the squamosal. The diverticulum D 2 (of Hürzeler) appears to lie outside this suture. If then, as Hürzeler suggested, the alisphenoid forms no part of the anterior bulla wall, this diverticulum (D 2) is extra-bullar. The broad overlapping of the external pterygoid plate of the alisphenoid onto the anterolateral bulla wall in *Necrolemur* (Fig. 2) is a feature of some interest in relating the Quercy form to the modern *Tarsius*. Cope (1885:467) long ago stressed the distinctiveness of this region of the tarsier basicranium when comparing it with the then newly discovered skull of an American Wasatchian prosimian, *Tetonius homunculus*. In both *Necrolemur* and *Tetonius* these external pterygoid plates overlap the bullae, as in *Tarsius*. Gregory (1920:227) gives the following as a general character of lemuroid Primates: "The elongate pterygoid plates of the alisphenoids extended back to the auditory bullae, whereas in the Anthropoidea they are well separated from them." A further distinction here is possible in that the posterior extremities of the external pterygoid plates in lemurs and lorises, including such fossil forms as *Smilodectes, Notharctus, Adapis,* and *Pronycticebus,* typically (although not in all cases) reach back to the anterior tip of the bulla, but the area of contact is very small and cannot be described as overlapping. *Necrolemur, Tarsius,* and *Tetonius* differ in this respect

from lemuriform, lorisiform, platyrrhine, and catarrhine Primates.

Stehlin could not find the stylomastoid foramen in his specimens; Hürzeler (1948) shows it in figures 27 and 28 at the posteroexternal angle of the bulla, but does not label it (see Fig. 1). Just anterior to this foramen is a fossette, probably for reception of the stylohyal, if, as in *Tarsius*, the tympanohyal was not distinct (van der Klaauw, 1931:239). This foramen and fossette lie in the same depression and have a somewhat variable degree of separation. In M.C.Z. 8879 the external appearence is as a single oblong foramen, while in Paris 1 the two are more distinctly set off (Fig. 2). A specimen at the British Museum is intermediate in this regard.

Contrary to Stehlin's suggestion (1916:1348) that a true postglenoid process does not exist in *Necrolemur*, Paris 1 and 5 exhibit a process that can justly be termed postglenoid. Also a postglenoid foramen is present (M.C.Z. 8879, Paris 1, 2 and 5) median to this process and between the posterior limit of the glenoid area and the external auditory tube.

Two large foramina, one on either side of the alisphenoid pterygoidal wing, were described by Stehlin (1916:1353-1354) as the inner and outer openings of the canalis civinninii (or foramen pterygospinosum, Stehlin 1912:1205). He named a smaller opening situated anterodorsally in the same region the foramen ovale. The position of this latter small foramen is variable, but is always anterior to the glenoid fossa instead of being approximately on a line with it, as is the foramen ovale in Primates generally. In those specimens in which this foramen is relatively large, a groove extends laterally and slightly posteriorly from it, which would probably not be the case if it were the foramen rotundum. Removal of matrix from Paris 1 and 2 in the region of the external pterygoid plate or wall has revealed a foramen opening directly into the cranial cavity, lying within the wall at the juncture of canals from the three foramina. Given this information, probably not known to Stehlin, we suggest that the posteroexternal foramen (outer opening of Stehlin's canalis civinninii) is the foramen ovale.

In a footnote, Stehlin (1916:1354) cited Gregory (1915:430) as confirming his identifications in the region of the foramen ovale. Gregory does this only partially, committing himself no further than to say that the foramen ovale is on the external (as opposed to the internal) side of the external pterygoid wall.

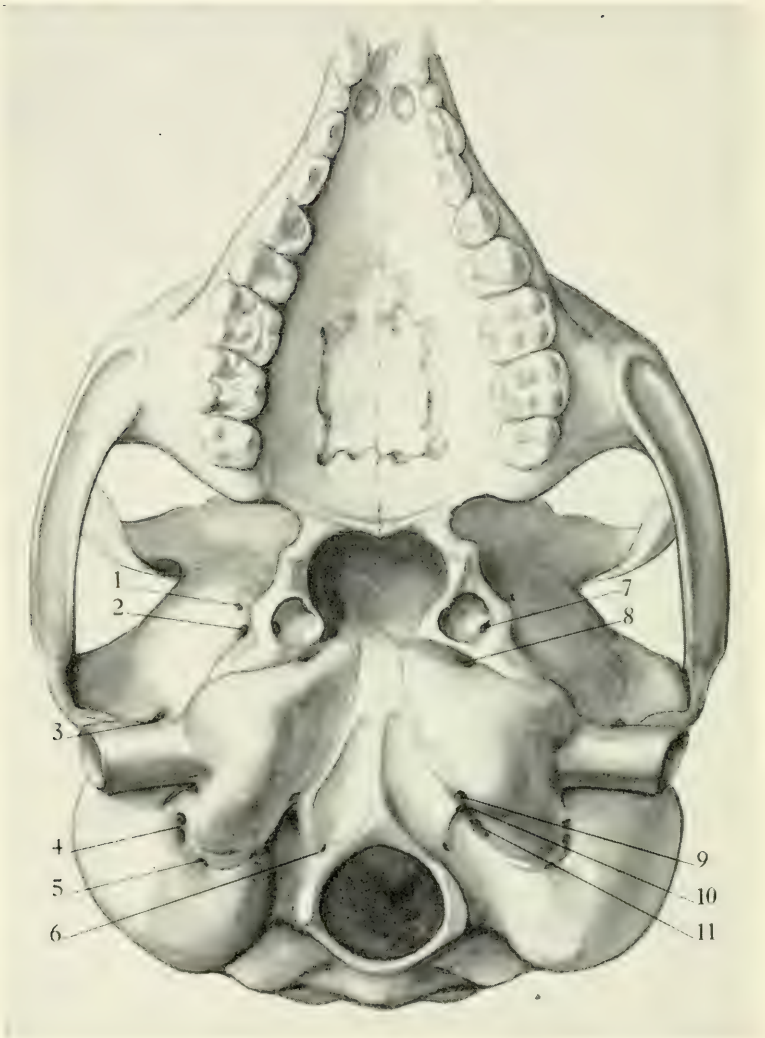

FIGURE 2

Necrolemur antiquus x 3.5

1. Foramen for branch of internal maxillary artery
2. Foramen ovale
3. Postglenoid foramen
4. Stylomastoid foramen and fossette for ? stylohyal
5. Foramen for auricular branch of pneumogastric
6. Hypoglossal foramen
7. Alisphenoid canal
8. Opening of eustachian tube
9. Internal carotid foramen
10. Inferior petrous sinus
11. Posterior lacerate foramen

He did not definitely say that Stehlin's small foramen is the foramen ovale. However, he identified as the foramen rotundum the smaller foramen (Stehlin's f. ovale) regarded by us as being for the internal pterygoid branch of the internal maxillary artery.

III. ORBIT

Along its median wall the orbit is composed principally of the frontal and the maxillary. Careful search of Paris 1 revealed no os planum present in the orbital wall (Fig. 3). The lacrymal forms a narrow band within the orbit along the anterior rim. Frontal, parietal and alisphenoid comprise the posterior wall. No anterior sutures between the small orbitosphenoid, frontal, and palatine, respectively, could be made out in Paris 1, in which this region is entirely undistorted. Only a small palatine component is present in the orbit, and this does not separate the frontal from the maxillary.

Stehlin (1916:1345) noted that his material was not adequate to allow determination of the maxillo-malar suture. This led him to suggest that the malar might reach the lacrymal. Paris 1 and 2 show that this is not the case; the maxillary makes up part of the orbital rim. When discussing the Eocene lemuroid *Notharctus,* Gregory (1920:227) remarked ". . . the malar if not in actual contact with the lacrymal certainly came very close to it, whereas in tarsioids and anthropoids it becomes widely separated from the lacrymal and limited to the outer side of the orbit." Consequently, *Necrolemur* resembles the higher Primates in this regard, and not the majority of prosimians other than *Tarsius.*

The absence of an ethmoid component in the rostral orbital wall of *Necrolemur* has been taken by some students as an indication of a lack of affinity between it and *Tarsius,* since in the latter the os planum is large. To the writers this distinction does not seem to have much significance. A primitive prosimian condition, where the ethmoid has no orbital plate, is retained in such forms as *Necrolemur, Pronycticebus, Smilodectes* etc., in which, perhaps, there has not been enough orbital expansion to effect an expression of this bone in the orbit by impinging on the anterior part of the interorbital septum. In *Tarsius* and some Lorisiformes the interorbital septum is very narrow — evidently an accommodation for relatively large eyes, and in both groups an os planum occurs. Moreover, only in Cheirogaleinae,

among living and fossil Lemuriformes, is the os planum present. In these small lemurs also, the occurrence of an os planum is coupled with large orbits (compared to body size) and a thin interorbital septum. For the Anthropoidea, a similar origin for

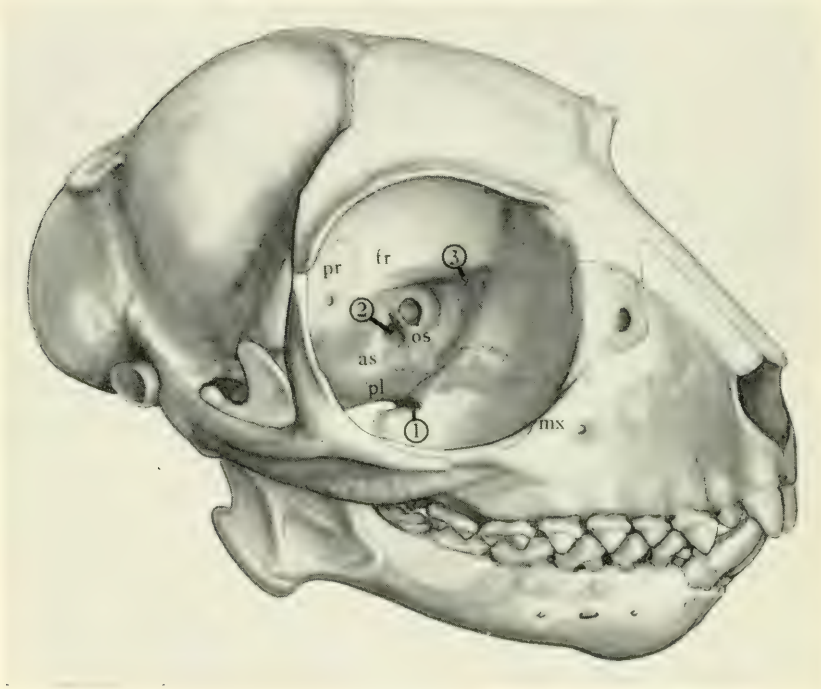

FIGURE 3
Necrolemur antiquus x 3.5 approx.

1. Sphenopalatine foramen and posterior palatine canal
2. Foramen rotundum and anterior lacerate foramen (?coalesced)
3. Ethmoid foramen

Abbreviations:
as, alisphenoid
fr, frontal
mx, maxilla
os, orbitosphenoid
pl, palatine
pr, parietal

this orbital element may be considered. In most Ceboidea the orbits restrict the interorbital septum to a thin plate on which the os planum is exposed laterally. Although in Old World Anthropoidea the rostrum between the orbits is occasionally

rather broad, it is possible to posit that such breadth is secondary and that they descend in common from a form in which relatively large eyes impinged on the interorbital area enough to induce the appearance of an orbital ethmoid component. This hypothesis is strengthened by observed interorbital narrowness in the only known part of an Oligocene catarrhine skull (Simons, 1959:8). If the foregoing suggestions apply, then it is not necessary to expect the presence of an os planum in the stock from which *Tarsius* may have arisen.

In *Necrolemur* (Paris 1), a small venous foramen can be seen situated near and beneath the median dorsal rim of the orbit. As in *Tarsius,* but apparently not in other Primates, below this foramen a deep groove curves posteroventrally and (in both) lies at a juncture between the plane of the lateral wall of the rostrum and that of the back of the orbit. This is another unusual feature (occurring in both *Necrolemur* and *Tarsius*) which has to be attributed to independent acquisition, by those who doubt that any known fossil prosimians have a close phyletic relationship to *Tarsius.*

A cranio-orbital foramen exists in Paris 1, but could not be found in Paris 2, 3 or 5. Running anteroposteriorly and slightly above the optic foramen is another groove. A small opening near its anterior end appears to be the ethmoid foramen. The sphenopalatine foramen and the posterior palatine canal in Paris 1 are combined to open posteriorly through a common large foramen in the suture between maxillary and palatine.

Apparently coalescence of the foramen rotundum and the anterior lacerate foramen occurs in Paris 1 but they are separate in Paris 5. In both cases, however, the foramen rotundum lies within the orbit, as Stehlin noted (1916:1353), and not lateral to the postorbital part of the alisphenoids, as Gregory (1915:430) suggested.

The orbital region of Paris 1 is entirely undistorted and shows that the postorbital opening was small. It is of some interest that neither lemurs nor lorises, nor any other known fossil prosimians of similar size possess a smaller aperture here. As with so many cranial characters the primate showing the most interesting resemblance to *Necrolemur* in respect of the structure of the postorbital region is *Tarsius.* However, because of the huge flanges that encircle the orbit in mature specimens of *Tarsius,* and the greater degree of postorbital closure seen in such adults, much more revealing comparisons can be made between skulls of

Necrolemur and those of juvenile tarsiers. In the latter, the circumorbital flanges are not yet very pronounced and resemble the slight flanges seen in *Necrolemur* (Fig. 3). It seems necessary to assume, first, that these flanges in *Tarsius* are concerned primarily with the support of the enormous eyes, and second, because of their very uniqueness, that they were not so developed in Eocene forerunners of the living genus. *Necrolemur* clearly has such flanges in an incipient stage.

Closure behind the orbit in *Tarsius* (on the outside) can be seen to proceed in successively older juveniles from three main centers: 1, ventrolaterally, by an upgrowth of the posterior midregion of the orbital plate of the maxilla; 2, laterally, by an anteroposterior spreading of the middle of the postorbital bar; and 3, dorsolaterally, by growth of a flange from the frontal, which arises beneath the frontal insertion of the postorbital bar. Ossification proceeds downward as this flange, or plate, grows alongside the postorbital bar, and it eventually fuses with the bar, leaving no sutural indication. In most specimens of adult *Tarsius*, the frontal and jugal components of the postorbital wall can be distinguished by the fact that the region where they fuse is much thinner and consequently more translucent. In *Necrolemur*, at least two of these components effecting closure appear to be partially developed. Paris 1 has an uncrushed postorbital bar which shows an anteroposterior spreading at the middle, much as in *Tarsius*. The evidence is less clear because of breakage, but the posterior part of the orbital plate of the maxilla also bears a flange in *Necrolemur*. The third center of closure seen in *Tarsius*, the frontal element, is indicated in *Necrolemur* only by a distinct angulation along the lateral wall of the cranium betwen the orbital and temporal fossae. Although such characters as the greatly reduced paraconids and the loss of certain anterior lower teeth eliminate *Necrolemur* from the direct ancestry of *Tarsius*[1], the incipient circumorbital flanges and characteristics of postorbital closure in *Necrolemur* are suggestive of a stage to be expected in the *Tarsius* ancestry. Perhaps *Pseudoloris* or *Nannopithex* are nearer the actual line leading to the modern form, but incompleteness of known specimens prevents the sort of comparisons here made with *Necrolemur* and leaves this possibility insoluble at present.

[1] Even if this were not so it would be almost irrelevant, in the absence of intermediates, to urge an ancestor-descendent relationship for forms so separate in geographic distribution and in time.

It may be noted in passing, that the manner of postorbital closure in *Tarsius* (insofar as the malar and frontal are concerned) is distinct from that seen in catarrhines and platyrrhines. Closure in this area in *Tarsius* is chiefly effected by an outward and downward growth of a flange of the frontal (with relatively little malar expansion) while in higher Primates the greater part of the dorsolateral area of enclosure is contributed by the development of an orbital plate of the malar. These differences strongly imply that the partial postorbital closure of *Tarsius* only parallels that of the Anthropoidea and is not a character of their common inheritance. If it be agreed that some postorbital closure arose at least twice among Primates, the possibility that this feature also was independently acquired in the ancestral platyrrhine and catarrhine stocks can be more seriously entertained.

EXPLANATION OF FIGURES

The lateral and ventral views of the skull of *Necrolemur* are based on Paris 1, to which details of missing regions have been added from other specimens, principally M.C.Z. 8879. Misleading stains and fractures in Paris 1 are largely omitted from these illustrations. Certain details of the anterior dentition and mandible are drawn from specimens figured by Stehlin (1916).

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B R E V I O R A

Museum of Comparative Zoology

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SIZE OF ENDOCEROID CEPHALOPODS[1]

BY CURT TEICHERT[2] AND BERNHARD KUMMEL[3]

The maximum size of fossil animal groups, whether mammals, reptiles, or invertebrates has always been a fascinating subject of inquiry, because phyletic size increase is one of the important trends that dominate the evolution of living things. In the case of large animals, the evidence is often hard to assemble because their remains are difficult to obtain, to transport, and to store. Squids are the largest living invertebrates and a tradition has been handed down in paleontological literature that the largest fossil invertebrates likewise are to be found among the cephalopods, but few accurate data are to be found in published sources which are now readily available.

Among the nautiloid cephalopods, it has long been suspected that the Endoceratida furnished the real giants, but no accurate measurements in support of this statement are available.

Clarke (1897) stated that entire shells of *Cameroceras proteiforme*, 10 to 15 feet long (3 to 5 meters), had been found in the Middle Ordovician of Minnesota. In the same publication, Clarke figured an internal cast of part of a siphuncle, from the base of the body chamber to the adapical end of the spiess, which was 3 feet and 3 inches long. Miller and Kummel (1944) described and illustrated additional species of these Middle Ordovician endoceroids from Minnesota, which are deposited in the Carnegie Museum. One of their paratypes of *Endoceras clarkei* measured 750 mm long, is septate throughout and is not complete, adapically or adorally. The holotype of *Endoceras gracillimum* Miller and Kummel (1944) measured 670 mm in

[1] Publication authorized by the Director, U. S. Geological Survey.

[2] U. S. Geological Survey, Denver, Colo.

[3] Museum of Comparative Zoology.

length, again an incomplete specimen consisting only of phragmocone. These same authors described a new species, *Endoceras decorahense*, on two portions of the internal mold of the phragmocone from the Decorah formation, Winneskiek County, Iowa. The larger portion is about 625 mm long and the length of the smaller measures about 320 mm. They estimated the interval between the two pieces as about 115 mm, so the total length of this phragmocone was about 1,060 mm. These authors also mentioned that there is on display in the Chicago Natural History Museum a larger endoceroid that measures 6 feet in length.

Teichert (1927) noted the occurrence, in Middle Ordovician limestones of Estonia, of endoceroids as much as 5 meters long, but gave no further details. Flower (1955) stated that specimens 12 feet in length had been collected and added that he was "not wholly inclined to discredit a report of an endoceroid found in a quarry near Watertown, New York, which was measured before it was broken up and found to attain a length of 30 feet." As far as we have been able to ascertain, these somewhat vague statements are all that is presently available in the published record on the subject of the maximum size of endoceroid cephalopods.

It does not seem to be generally known that the Museum of Comparative Zoology at Harvard University possesses what appears to be the largest fragment of an endoceroid cephalopod on display anywhere in the world. As Flower (1955) has stated, "the removal of even reasonably complete specimens involves something very close to quarrying operations, storing them is another problem." The specimen in the collections of the Museum of Comparative Zoology is, therefore, probably unique in museums of the world.

The specimen measures 3,000 mm in length but is not complete, adorally or adapically. In general the preservation is fair, but as a result of weathering and crushing the full diameter of the conch is preserved only in one plane, and in the other plane the outer shell is removed exposing traces of septa and in places the siphuncle. The first recognizable septa are 500 mm from the adoral end but the whole specimen could well be phragmocone as this adoral 500 mm is slightly crushed and weathered and one cannot tell whether septa are present or absent. The adoral diameter of the specimen is 280 mm. The conch tapers at a uniform rate and the adapical diameter measures 120 mm.

Figure 1 — Large endoceroid on exhibit in the Museum of Comparative Zoology.

The septa slope adapically at an angle of about 45° and in the mid-part of the specimen are spaced 17 to 20 mm apart. The siphuncle is visible only on the adapical half of the specimen. About 1,000 mm from the adoral end of the shell the siphuncle has a diameter of about 95 mm; at 1,750 mm from the adoral end of the shell the siphuncle has a diameter of 75 mm. The first endocones appear 2,000 mm behind the adoral end of the shell. The spiess measures 510 mm in length. The surface of the shell bears faint annulations that are spaced approximately 10 to 12 mm apart.

SUMMARY OF MEASUREMENTS

Length	3,000 mm
Adoral diameter	280 mm
Diameter 1,000 mm from adoral end	220 mm
Diameter 1,750 mm from adoral end	170 mm
Adapical diameter	120 mm
Diameter of siphuncle 1,000 mm from adoral end	95 mm
Diameter of siphuncle 1,750 mm from adoral end	75 mm
Spiess length	510 mm

A graphical reconstruction of the shell on the basis of these measurements shows that the entire fossil from its presently preserved adoral end to the apex may have measured about 5,800 mm.

The total length of the body chamber is a matter of guesswork. There are few published and illustrated records of any straight fossil cephalopod shells, complete from apex to aperture, which are more than a foot or so long. In short shells the ratio of body chamber to phragmocone may be high, even larger than 1:1. With increasing total length of conch, however, ratio of body chamber to phragmocone is likely to decrease, although no definite figures can be stated. In a specimen of *Actinoceras beloitense* (Foerste and Teichert, 1930, pl. 28), which was 450 mm long, the ratio of body chamber to phragmocone was about 1:2. Leith (1942) described a specimen of *Lambeoceras lambii* (Whiteaves) which was 45.5 in. (1,155 mm) long. He estimated the total length of the shell at 1,405 mm. The body chamber was almost wholly preserved and not more than 250 mm long. Ratio of body chamber to phragmocone was thus 1:4.6 in this specimen.

It should be noted, however, that both *Actinoceras beloitense* and *Lambeoceras lambii* have body chambers with constricted

apertures, whereas no endoceroids with constricted apertures are known. It seems physiologically plausible that in large straight cephalopod shells the animal should have a better "grip" on a body chamber with constricted aperture than on one with an unconstricted aperture; therefore, in shells which expanded uniformly from the apex to the aperture, like the endoceroids, the animal itself, and thus its body chamber, should have been relatively larger.

In a juvenile specimen of a straight ammonoid, *Baculites ovatus*, Trueman (1941) determined the ratio of length of body chamber to phragmocone as 1:0.7, but in adult shells this ratio becomes much smaller. If we assume the ratio of length of body chamber to phragmocone in endoceroids to be more like that of *Actinoceras beloitense* we arrive at a length of the body chamber for the Harvard *Endoceras* of 2,650 mm and for the entire shell of 8,150 mm, or 28 feet. This is a conservative estimate, yet close to the possible maximum figure of 30 feet mentioned by Flower.

Add to this the length of the tenacles which must have extended a considerable distance in front of the aperture, certainly no less than half the length of the body chamber, and we have an invertebrate animal considerably longer than 30 feet — a truly imposing size. Today's giant squid, *Architeuthis*, rivals and slightly exceeds in length the largest extinct endoceroids. Spärck (1928) records specimens of *Architeuthis dux* from the North Atlantic, washed ashore on the Norwegian Coast, that have body lengths of up to 2 meters and tentacles as much as 10 meters long. The largest specimen to our knowledge is that of *Architeuthis harveyi?* recorded by Verrill (1879, p. 196) which measures 624 inches (17 meters). There is a model in the Museum of Comparative Zoology of a specimen of *Architeuthis princeps*, which was washed ashore in Newfoundland, which measures about 15 meters in length. More recently, Lane (1960, pp. 198-227) has critically reviewed a larger number of reports of finds of and encounters with giant squids. He is inclined to believe that individuals of *Architeuthis* or some other genus, as yet undescribed, may reach overall lengths of some 70 feet.

While the Harvard specimen represents by far the largest nautiloid cephalopod on which accurate data are now available, it is interesting to compare it with the largest ammonoid on record. This is *Pachydiscus seppenradense* Landois from the

Upper Cretaceous of western Germany (Landois, 1895, 1898). In 1895, Landois first described this fossil ammonoid whose shell was 1,800 mm in diameter and in which the last camera was 550 mm high. Landois' reconstruction provided the animal with a body chamber equivalent to only one-fourth of a complete whorl. From this he concluded that the total diameter of the complete specimen of his ammonoid had been about 2,550 mm. From later studies (Trueman, 1941) it is, however, likely that Landois' estimate of the length and bulk of living chamber was too low. If the body chamber of *Pachydiscus seppenradense* was equivalent, as is more likely, to three-fourths or one full volution of the shell, the diameter of the adult shell of this ammonite would have been of the order of 3,500 mm, or more than 10 feet. A very approximate graphic plot of a shell of this kind shows that the total length of the shell of *Pachydiscus seppenradense*, when unrolled, would have been of the order of 60 feet, or roughly twice as long as that of the largest endoceroid.

In another paper Landois (1898) attempted to estimate the weight of these giant cephalopods. On the basis of his estimated measurements he arrived at a total weight of the ammonite as 1,455 kg, or 750 kg for the weight of the animal itself, and 705 kg for the weight of the shell.

We shall abstain from any attempt to indicate exact weights of the large endoceroids. The order of magnitude was almost certainly the same as that inferred by Landois for the giant *Pachydiscus*, something of the order of 1 ton (about 1000 kg). It must be assumed that the weight of shell and siphuncle, which for a length of over 5,000 mm was entirely filled with calcareous deposits, balanced the buoyancy provided by the empty camerae and confined the animal to a strictly benthonic existence. Few, if any, fossil invertebrates ever surpassed them in bulk weight and size.

One other point deserves attention: Phyletic size increase is a trend that as a rule continues until the end, or very close to the end of the evolutionary life of a particular group of organisms, as, for example, in the ammonoids. The endoceratids, however, reached their maximum size long before the time of extinction, in fact relatively early in their evolution. In North America, as well as in northern Europe, endoceroid cephalopods survive to the end of the Ordovician period, but reach their maximal size during Middle Ordovician time (Teichert, 1930, pp. 235-236).

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BREVIORA

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TYPE AND TYPE LOCALITY OF THE GULF COAST SPINY SOFTSHELL TURTLE, TRIONYX SPINIFER ASPER (AGASSIZ)

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The currently accepted type locality of *Trionyx spinifer asper*, Lake Concordia, Louisiana, is in an area of intergradation between three subspecies of *Trionyx spinifer*. Of the nine available syntypes of *asper*, none has been designated as a lectotype, and only one of the syntypes of *T. s. asper* is recognizable as belonging to that taxon.

Abbreviations of names of museums from which specimens are mentioned are: KU, Museum of Natural History, University of Kansas; MCZ, Museum of Comparative Zoology, Harvard College; SM, Strecker Museum, Baylor University; TU, Tulane University; and USNM, United States National Museum.

Agassiz (1857:406) described *Aspidonectes* (= *Trionyx*) *asper* as having:

> ". . . very coarse and large tubercles of the front and hind part of the carapace, which extend, behind, even over the bony shield, and are there supported by prominent warts of the bony plates. These bony warts exist in no other species with which I am acquainted: their form is very irregular, sometimes oblong and sometimes orbicular; they also project more or less. Another marked peculiarity of this species consists in the greater bluntness of the extremities of the jaws, which are more rounded than in Asp. spinifer. The jugal arch is also broader. The difference between the males and the females is more striking in this species than in any other, the males being regularly oval, whilst

> the females are almost circular in their outline . . . in younger specimens of Asp. asper there are . . . two or three black lines separating the pale rim of the posterior margin, . . .''.

Several of the syntypes show ''prominent warts of the bony plates'' (*supra*), which appear posteriorly and principally on the seventh pair of pleurals toward the midline on the bony carapace (Plate 1). I have seen bony elevations, which are circular or elongate resembling short ridges, on the carapaces of specimens of *Trionyx ferox* (USNM 4373, 55316, 62217); a photograph of a *ferox* (Stejneger, 1944:pl. 7) clearly shows bony prominences on the posterior part of the bony carapace. These bony elevations also occur in populations of *T. spinifer* (SM 2552, 2558, Texas; USNM 54731, Iowa; USNM 100396, 100404, Louisiana). Bony warts and ridges on the posterior part of the carapace are not diagnostic for *T. s. asper*. To my knowledge, the subspecies of *Trionyx spinifer* are not distinguishable by characteristics of the skull, bony carapace or plastron.

T. s. asper closely resembles the subspecies *hartwegi* and *spinifer* but differs in usually having two or more blackish lines paralleling the rear margin of the carapace, and usually in having the postocular and postlabial stripes united on the side of the head. Other characters mentioned above by Agassiz seem not to be of taxonomic worth.

Agassiz (*op. cit.*:405-06) did not designate a type, mention precise localites, or state the number of specimens that formed the basis of his description of *Aspidonectes asper*. Baur (1893: 220) restricted the type locality of *asper* to Lake Concordia, Louisiana, but did not mention any specimens; presumably Baur's action was based upon an examination of the bony carapace of USNM 012349, which shows the prominent bony ridges described and considered diagnostic by Agassiz and has ''Lake Concordia, Louisiana'' written in ink on the underside of the carapace. Barbour and Loveridge (1929:225) listed MCZ 1597 and 1622 as cotypes. Stejneger (*op. cit.*:56-58) discussed some of the syntypes of *asper*, and also regarded the type locality as ''Lake Concordia, La.,'' designating USNM 12349 (= 012349) and MCZ 37173 as ''cotypes.'' The type locality of *T. s. asper* is currently accepted as Lake Concordia, Louisiana (Schmidt, 1953:109).

T. s. asper intergrades with *T. s. hartwegi* and *T. s. spinifer* in the lower Mississippi Valley (Conant and Goin, 1948:11).

The softshell turtles inhabiting the Mississippi River and its tributaries in Louisiana (including Lake Concordia) and Mississippi represent an intergrading population of *spinifer* and *hartwegi*, and, to a lesser extent, *asper*. Most turtles from the Pearl River drainage and rivers that drain into Lake Pontchartrain adjacent to the east are typical of *asper*. Lake Concordia is a large oxbow on the west side of the Mississippi River in Concordia Parish, Louisiana. I was a member of a field party, from Tulane University, which collected three specimens (TU 16524, 16524.1, 16524.2) of *Trionyx spinifer* from Lake Concordia on August 1-3, 1954. Because none of these turtles has the postocular and postlabial stripes united on the side of the head or any indication of more than one marginal line paralleling the rear margin of the carapace, none is considered referable to *asper*.

Some of the nine syntypes discussed below were mentioned by Stejneger (*op. cit.*:57-58).

(1) USNM 012349 (Plate 1) is represented by a bony carapace and may be considered the present type (lectotype), although never designated as such. "Trionyx Ferox?, Lake Concordia, Louisiana, BLC Wailes, 1851" is written in ink in the same handwriting on the underside of the bony carapace. Subsequently, "Ferox?" has been crossed out and "asper" added in pencil, and "012349" inked on the second pleural. A gummed label is pasted on the fifth rib, right side, and bears the inscription "asper Ag. (Type)." There is also an attached metal tag bearing the number 22676. The carapace has a maximal length of 14.9 cm. and width of 12.7 cm.; its size suggests that it is that of a female. On the seventh pair of pleurals and in line with the longitudinal sutures of the neurals are two, short, longitudinal, elevated, bony ridges.

(2) USNM 01086 is represented by an intact bony carapace (19.8 cm. in length and 16.5 cm. in width), disarticulated parts of the bony plastron (epiplastron and preplastra lacking), and a skull including the lower jaw. There is an attached paper tag labeled "cotype." "Miss." is written in ink on the underside of the carapace. There are small, slightly-elevated bony warts on the sixth pair of pleurals (with few, less conspicuously developed, on the seventh pair), and a semblance of ridging as seen on the carapace of USNM 012349. "Washington Lake" (crossed out in pencil), and "1086" are written in ink on the skull, which has a basicranial length (occipital condyle to tip

of upper jaw) of 62.8 mm. The locality "Washington, Adams Co." is written in pencil on the card for USNM 01086 in the card file in the USNM. The specimen is certainly a female judging from the size of the skeletal parts.

(3) USNM 01084 is represented only by the skull (lacking lower jaw) of a female, which has a basicranial length of 63.1 mm., and the number "1084" and "Wash." inked on it. The skull is presumably from the same locality as USNM 01086.

(4) MCZ 46621 is represented only by the skull (lower jaw present) of a female having a basicranial length of 63.0 mm.; it was received from B.L.C. Wailes.

(5) MCZ 1622 has been photographed by Stejneger (*op. cit.*: pl. 16), who mentioned a label in lead pencil, "No. 1622. *Type* Amyda asper (Agassiz) Lake St. John, Miss. W. Sargent leg. et don." (which I have not seen) (*op. cit.*:58). Stejneger suggested that Lake St. John was in Louisiana (*op. cit.* :footnote 2); however, the caption for Plate 16 reads Lake John, Florida. Goin (1948:304), commenting on the last-mentioned locality, wrote that MCZ 1622 ". . . is listed in the museum catalogue as having come from Lake St. John, Mississippi." Lake St. John is a few miles north of Lake Concordia occurring in Concordia and Tensas parishes, Louisiana, in the Mississippi River drainage.

MCZ 1622 is a young alcoholic specimen, probably a female, having a plastron 5.0 cm. in length, and a carapace 6.8 cm. in length and 6.0 cm. in width. The postlabial and postocular stripes do not join on either side of the head. The undersurface is more heavily pigmented than that which I judge to be "normal" for *T. s. asper*. The most significant character is the lack of more than one dark marginal line posteriorly on the carapace; there are small blackish dots posteriorly but these are widely-separated and not closely-set in a linear fashion to suggest a second marginal line. Neill (1951:19-20) believed this specimen to show ". . . some approach to *spinifera*." I do not regard this specimen as representative of *T. s. asper*.

Schwartz (1956:15), however, referring to MCZ 1622, stated that it ". . . differs in no way, so far as head and carapace pattern is concerned, from similarly sized specimens of *T. s. agassizi* (= *asper*) from South Carolina and Georgia." It would be surprising to find specimens from South Carolina and Georgia having a pattern on the carapace resembling that of MCZ 1622; Schwartz's photograph of a juvenile from South Carolina (*op. cit.*:14, pl. 3) is certainly *asper*.

(6) MCZ 46633 bears the locality "Washington, Mississippi" written in ink on an attached paper tag. In a different hand, the data "Washington, Miss. Pres. by B. L. C. Wailes" and the number "9" is written in ink on an unattached, folded piece of stiff, brownish paper that is held in place by a metal rod against the plastron. The data suggest that this specimen is from the same locality as USNM 01084 and 01086.

MCZ 46633 is a stuffed, adult male having a plastron approximately 11.0 cm. in length and a carapace 16.0 cm. in length. The postlabial and postocular stripes fail to join by a narrow segment on the left side of the head, but appear to be in contact on the right side. Bony, longitudinal welts, resembling those on the bony carapace of USNM 012349, appear posteriorly on the seventh pair of pleurals. The carapace is darkened laterally and sprinkled with widely-spaced, black dots; there is no indication of a second marginal line. The pattern on the carapace most closely resembles that of *T. s. hartwegi.* Therefore, I do not consider this specimen to be representative of *T. s. asper.*

(7) MCZ 46615 bears an attached label having the following data written in ink: "Trionyx ferox SOUTHERN SOFT-SHELLED TURTLE Natchez, Miss. H. Wheatland coll'n." Subsequently "Trionyx ferox" has been crossed out and "Amyda aspera" written in ink; the name "spinifera" also has been added in pencil. The reverse side of this label bears the number "8" and the name "B. Chase" written in pencil. A small piece of paper also bearing the number "8" is pasted on the left side on the bony carapace. Presumably this specimen has some relationship to MCZ 46633 that bears the number 9.

MCZ 46615 is a large, stuffed adult female having a plastron that measures approximately 33.0 cm. and a carapace 43.0 cm. in length; the anterior edge of the carapace is studded with conical tubercles. Scattered, oblong, bony elevations adorn the seventh pair of pleurals. There is no pattern evident on the carapace, and the striping on both sides of the head is obscure. This large female might represent any of the subspecies *spinifer, hartwegi* or *asper;* there is no character that identifies the specimen as *T. s. asper.*

(8) MCZ 37173 is the stuffed specimen that Agassiz mentions having received from the University of Oxford (at Oxford, Lafayette County), Mississippi (*op. cit.*:405); the specimen is discussed by Stejneger (*op. cit.*:57). The plastron is approximately 23.5 cm. in length; the length of the carapace, wrinkled

posteriorly, measures (in a straight line) approximately 29.5 cm. Although the tail extends noticeably beyond the posterior edge of the carapace and is presumably the basis for Stejneger referring to MCZ 37173 as an adult male, its large size indicates that it is a female. A red paper label bearing the writing "A. asper Ag. Cotype" is pasted on the plastron. Elevated bony knobs appear toward the posterior margin of the bony carapace on the seventh pair of pleurals. There are well-defined stripes on the head, but the relationship of the postocular and postlabial stripes is obscure. There is no evidence of more than one dark marginal line paralleling the rear margin of the carapace. Hence the specimen is not recognizable as *T. s. asper*.

(9) MCZ 1597, a large alcoholic female, is considered representative of *T. s. asper* (Plate 2). A paper label on the left foreleg bears the inscription "Natches, Miss W. Sargent." The carapace, measuring approximately 43.0 cm. in length and 37.0 cm. in width, has more than one dark marginal line and several ocelli. Inner marginal lines in the posterior right and left quadrants are mostly continuous, but are obscured by the wrinkling and scratching on the posterior part of the carapace. The tubercles on the anterior edge of the carapace are worn and resemble rounded knobs; more lateral tubercles are equilateral. The seventh pair of pleurals are in contact medially behind the seventh neural. There are indications of raised bony welts on the last pair of pleurals. The head is partly extended, but does not show the relationship of the stripes on the side of the head. The pattern on the snout is obscured, and blackish marks are evident on the dorsal surface of the limbs. The plastral surface lacks dark markings and measures approximately 32.5 cm. in length. MCZ 1597 is discussed by Stejneger, who mistakenly refers to the specimen as a male (*op. cit.*:58). MCZ 1597 (Plate 2) is herewith formally designated as lectotype of *Trionyx spinifer asper* (Agassiz), as it alone, of the nine specimens hitherto considered syntypes of *Aspidonectes asper* Agassiz, is recognizable as referable to the subspecies *asper*.

Agassiz (1857:405) mentions having received specimens from Mr. Winthrop Sargent of Natchez, Mississippi (MCZ 1597, 1622, 46615), Dr. L. Harper of the University of Oxford, Mississippi (MCZ 37173), and Professor B. L. C. Wailes of Washington, Mississippi (MCZ 46621, 46623, USNM 01084, 01086, 012349). These localities suggest places of residence and are not necessarily localities at which the specimens were captured; at least two syntypes (MCZ 1622, USNM 012349) are from locali-

ties different from those mentioned immediately above. Although forwarded to Agassiz from Natchez, the specific locality from which the lectotype (MCZ 1597) was captured is unknown. Natchez, Oxford and Washington, Mississippi, are in the drainage basin of the lower Mississippi River, which is inhabited by softshells that are intergrades between *T. s. spinifer* and *T. s. hartwegi,* although few specimens from there are typical of *T. s. asper.* It is possible, but unlikely, that MCZ 1597 was captured at Natchez. Those syntypes having a discernible pattern on the carapace, which is not that of *asper,* probably came from tributaries in the lower Mississippi River drainage.

The lectotype, MCZ 1597, probably came from the Pearl River drainage (adjacent eastward from the Mississippi River drainage), where most individuals are representative of *T. s. asper.* Occasional specimens of *asper* from the Pearl River drainage have only one dark line paralleling the rear margin of the carapace, and resemble softshells occurring in the Mississippi River drainage. An adult male given to me by William E. Brode was stated by him to have come from the Pearl River; this turtle (KU 47120) has only one dark marginal line, and Stejneger (*op. cit.*:64) mentions another from the Pearl River drainage. Schwartz (*op. cit.*:16) and Crenshaw and Hopkins (1955: 20) write that some specimens from Georgia have only one solid line at the margin of the carapace. However, most of the softshells inhabiting the Pearl River drainage are typical *asper,* and the Pearl River drainage is probably the provenance of the lectotype, MCZ 1597.

The type locality of *Trionyx spinifer asper* (Agassiz), represented by the lectotype, MCZ 1597, is herewith designated as the Pearl River at Columbus, Marion County, Mississippi. The geographic range of *T. s. asper* (*Platypeltis agassizi* Baur considered a synonym) is the southeastern United States except peninsular Florida from the Florida parishes of Louisiana east to southern North Carolina; in streams of the Gulf Coast drainage including that of Lake Ponchartrain, Louisiana, eastward to the Apalachicola River system, and those of the Atlantic Coast drainage including that of the Altamaha River in Georgia northward to the Pee Dee River drainage in South Carolina.

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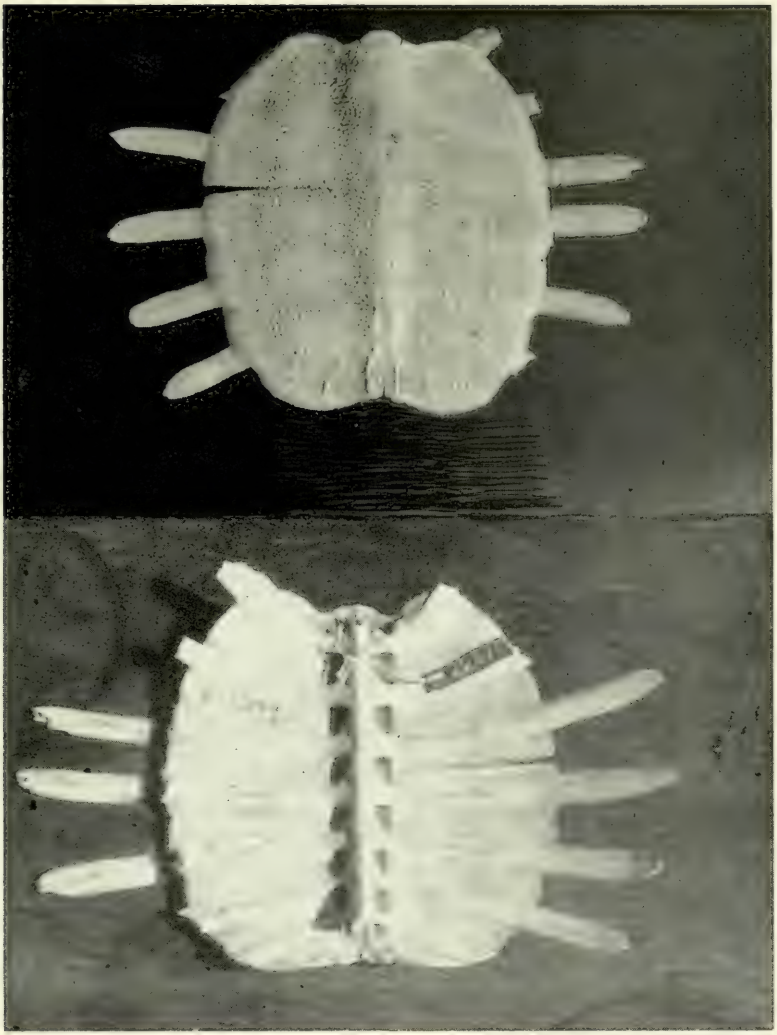

Plate 1 (× approx. ⅓). Bony carapace of *Trionyx spinifer*, USNM 012349, from Lake Concordia, Louisiana; parts of ribs that extend beyond carapace on right side are detached. *Top.* — Dorsal view showing elevated prominences posteriorly that Agassiz considered diagnostic for *Aspidonectes asper*. *Bottom.* — Ventral view showing inscriptions.

Plate 2 (× approx. 1/5). Dorsal view of lectotype of *Trionyx spinifer asper*, MCZ 1597; locality designated as the Pearl River at Columbus, Marion County, Mississippi.

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THE MECHANISMS OF CARAPACIAL AND PLASTRAL HINGES IN CHELONIANS

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Deraniyagala (1939) described the carapace and plastron of *Lissemys* and reported that there are two movable corselets in the carapace and four in the plastron. In the carapace the prenuchal is loosely connected to the anterior border of the nuchal by a thick ligament. This anterior corselet is moved downwards and acts as a valve. The last two marginals form a posterior movable valve in the carapace. In the plastron, the epiplastral lobe acts as an anterior plastral valve, and a small portion of the posterior part of the plastron demarcated by a transverse groove forms the posterior plastral valve. Besides these, there is a pair of cutaneous flaps which are used as valves to cover the posterior limbs after they are retracted under the shell. These flaps are known as the femoral valves. Presence of the cutaneous femoral valves is a distinguishing character of the subfamily Cyclanorbinae, in which the three genera *Lissemys, Cyclanorbis* and *Cycloderma* are grouped. Hasan (1941) worked out the shell-closing mechanism and described the principal muscles responsible for the movements of the six movable parts in *Lissemys*. George and Shah (1955), while working on the musculature of *Lissemys*, gave possible homologies of the muscles described by Hasan.

In the present study an attempt is made to describe the closing mechanism of the shell in most [1] of the chelonians in which part of the plastron or carapace is movable and acts as a valve. Care-

[1] No adult was available of *Notochelys platynota* in which an indistinct transverse hinge has been reported. Similarly there is only a juvenile at hand of *Pyxis arachnoides*. Siebenrock has described in this species a mobile anterior plastral lobe in which the entoplastron becomes involved. Since hinges only develop with age, it has not been possible to investigate hinge mechanisms in these species.

ful dissections of the muscles involved in the movements of the plastral lobes or the carapace parts were made of the following chelonians: *Cuora amboinensis, Emys orbicularis, Emydoidea blandingi, Terrapene mexicana yucatana, T. carolina carolina, T. c. baurii, T. c. triunguis, T. ornata, Testudo graeca, T. hermanni, T. kleinmanni, Kinixys erosa, Kinosternon baurii, K. cruentatum, K. flavescens spooneri, K. herrerai, K. leucostomum, K. scorpioides scorpioides, K. subrubrum, Sternotherus carinatus minor, S. odoratus, Cycloderma frenatum, Pelusios adansoni, P. carinatus, P. castaneus, P. nanus, P. subniger.* All specimens examined are in the collection of the Museum of Comparative Zoology.

Only two genera of the chelonians listed above, viz., *Cycloderma* and *Kinixys,* show some part of their carapace movable; the others have some part or parts of their plastra movable. In this regard all the chelonians used for the present study could be classified in four different groups:

The first group has only the anterior plastral lobe hinged and capable of valvular movements. The hinge is usually situated at the joint of hyo- and hypoplastral plates. The species of emydines examined show this condition.

The second group includes those that have only their posterior plastral lobes movable. The posterior plastral lobe is hinged at the level of the joint of the hypo- and xiphiplastral plates. This group is composed of the species of *Testudo* cited above.

The third group includes those which have both anterior and posterior plastral lobes movable. The kinosternines examined belong here.

The fourth group consists of the members of the subfamily Cyclanorbinae in which besides the movable anterior and posterior plastral lobes there are the two cutaneous femoral valves.

MOVEMENTS OF CARAPACE VALVES

In *Cycloderma* and *Cyclanorbis,* as in *Lissemys,* the prenuchal is movable. Hasan (1941) has described as the *M. nucho-prenuchalis* the muscle which is responsible for the movements of the prenuchal. This muscle arises from the under surface of the nuchal and is inserted on the posterior half of the under surface of the prenuchal. When this muscle contracts, the prenuchal is pulled downwards and acts as a small valve to close the shell after the head and the fore limbs are drawn under the shell and the anterior lobe of the plastron is lifted upwards. George and Shah

(1955) homologised this muscle with that part of the *spinalis-semispinalis* system occurring in this region. In no other chelonians are there such movable prenuchals.

The last two marginals in *Cycloderma* and *Cyclanorbis*, like those in *Lissemys*, are movable and act as a supracaudal valve. The *margino-infracaudales* are responsible for the downward pull (Hasan 1941). These muscles arise from the undersurface of the marginals and are inserted on the flexible subcaudal valve of the plastron. When these muscles contract the two movable marginals are pulled downwards and at the same time the subcaudal valve of the plastron is pulled upwards. The joint action of these two valves, i.e. the subcaudal and supracaudal valves, close the shell from behind and protect the tail and surrounding soft parts. These muscles are homologised with part of the *flexor caudae superficialis* by George and Shah (1955).

In *Kinixys erosa* an entirely different situation is present. Siebenrock (1916) has described the morphological features of the hinged carapace of this species in great detail. Briefly, however, it may be mentioned that the hinge is at the level of the fourth and fifth costal plates, the posterior part of the carapace being moved up and down like a valve at this point. This movement of such a large part of the carapace is unique to this genus.

The closing movement is brought about in the following manner. First the head and the neck are pulled under the shell as a result of the contraction of the *retrahens capitis collique*, the *rectus capitis cervico-plastralis* and *rectus cervicis* muscles. Of these muscles the *retrahens capitis collique* is the principal muscle responsible for the withdrawal of the head and the neck. The main part of this muscle in *Kinixys erosa* arises from the body of the seventh and eighth dorsal vertebrae and the undersurface of the costal plates near these vertebrae. The muscle inserts on the cervical vertebrae and on the base of the skull at its ventral side. After the head and neck are retracted fully, the muscle contracts still further and this additional contraction pulls the hinged posterior part of the carapace downwards and closes the shell from behind. In addition, the pelvic girdle muscles, i.e. the *attrahens pelvium*, also help in pulling the hinged part of the carapace downward. The *attrahens pelvium* is very highly developed in this genus and when it contracts the entire pelvic girdle is pulled forward, and since the girdle is firmly attached to the carapace the carapace is pulled with it. Although this pull is not so great as the one exerted by the *retrahens capitis collique*

it does contribute to the movement. A few muscles of the legs, i.e. the *ilio-tibialis* and *ilio-femoralis* which in part arise from the costal plate, also exert a pull on the carapace after the legs are fully retracted under the shell. Thus a combined pull resulting from the contraction of all these muscles is responsible for bringing about the valvular movements of the posterior hinged part of the carapace.

MOVEMENTS OF THE PLASTRAL LOBES

Anterior plastral valve: The anterior plastral lobe is hinged at the level of the hyo-hypoplastral joint in *Emys orbicularis*, *Emydoidea blandingii*, *Cuora amboinensis*, *Terrapene mexicana yucatana*, *T. carolina carolina*, *T. c. baurii*, *T. c. triunguis*, *T. ornata*, *Pelusios subniger*, *P. castaneus*, *P. carinatus* and *P. adansonii*. This anterior plastral lobe can be moved upwards like a valve which shuts off the shell in front after the head, neck and the fore limbs are retracted. This upward movement of the anterior plastral lobe is brought about in the following manner: After the head, neck and the fore limbs are retracted, the clavicular part of the *deltoideus* muscle contracts and pulls the plastral lobe upwards. The anterior part of the *pectoralis* muscle, which has its origin from the plastral lobe, also on contraction pulls the plastral lobe upward. Some part of the *scalenus* muscle which is inserted on the border of the plastral lobe helps in pulling the lobe upward. The precoracoid cartilage is attached to the entoplastral plate by a thick ligament and so when the whole girdle is rotated forward with the scapula acting as a fixed point the precoracoid and the coracoid which normally lie in a horizontal plane come now into an inclined plane with the precoracoid lifted upwards. Along with these the plastral lobe also gets pulled upwards and thus the rotation of the girdle helps in lifting the plastral lobe. These combined actions bring about the valvular movement of the anterior plastral lobe.

Normally the anterior plastral valve has a straight transverse hinge. This disposition of the hinge is very necessary for free valvular movements of the plastral lobe. But to this normal condition there is an exception in *Pelusios adansonii*. In this animal the hinge is not a straight transverse one but is V-shaped with the apex directed posteriorly. Because of this type of hinge the valvular movements of the anterior plastral lobe in this animal are very restricted compared to those possible with a straight transversely placed hinged.

Posterior plastral valve: A hinged posterior plastral lobe occurs in *Testudo kleinmanni*, *Testudo graeca* and *Testudo hermanni*. The hinge is at the level of the hypo-xiphiplastral joint and is also transversely placed. The posterior plastral lobe is pulled upward as a result of the contraction of the *retrahens pelvium* muscle of the pelvic girdle. This muscle arises from the spine of the pubis and is inserted on the entire inner surface of the xiphiplastral plate. In these animals the muscle is more highly developed than in forms which do not have a hinged posterior plastral lobe. Besides the action of the *retrahens pelvium* muscle the skin connecting the legs and the plastron exerts some pull on the plastral lobe which helps in pulling it upward.

Anterior and posterior plastral lobes: *Kinosternon subrubrum*, *K. flavescens spooneri*, *K. leucostomum*, *K. scorpioides scorpioides*, *K. baurii*, *K. cruentatum*, *K. herrerai*, *Sternotherus carinatus minor*, and *Sternotherus odoratus* possess anterior as well as posterior plastral lobes which are hinged and are capable of valvular movements. The upward movements of these two plastral lobes are brought about in the same way as described separately in the first two groups which had only one lobe, whether anterior or posterior, movable.

In *Kinosternon*, as far as the anterior plastral lobe is concerned, there is an additional factor pulling the plastral lobe upward. There are thick tendons which loosely connect the fourth, fifth and sixth cervical vertebrae with the plastral lobe. The point of attachment of these tendons on the plastral lobe is at the border of the epiplastral plates. When the head and the neck are pulled under the shell as a result of the contraction of the *retrahens capitis collique* (the main retractor of the head and the neck), an indirect pull is exerted on the plastral lobe because the latter is connected by thick tendons with the cervical vertebrae. Such a type of tendinous connection between the cervical vertebrae and the plastron is not met with in any of the other chelonians studied.

The *Terrapene* species examined have been placed in the first group in which only one anterior plastral lobe is hinged and movable like a valve. These species, however, require special attention since, although there is no true posterior plastral hinge, the posterior lobe is capable of being pulled dorsally and can close the shell posteriorly as efficiently as in those which have the posterior plastral lobe hinge. Here the bridge between the carapace and the plastron is very short and a large portion of the posterior part of the plastron is left unsupported. The *retrahens*

pelvium muscle in this animal is very highly developed and so when it contracts the posterior plastral border is lifted upward. This lifting occurs because the plastral plate bends under the pull exerted by the *retrahens pelvium* muscle. In this way, although there is no hinge at the level of the hypo- and xiphiplastral joint, the plastral plate closes the shell from behind, after the hind limbs and the tail are retracted within the shell.

Four plastral valves: The fourth group of the chelonians includes those which possess four plastral valves capable of valvular movements — the members of the subfamily Cyclanorbinae — *Lissemys, Cyclanorbis* and *Cycloderma.* Here the anterior plastral lobe is not as well demarcated and hinged as in the animals described above, but since the plastron is soft the movement is effected at the level of the posterior border of the entoplastral plate and the anterior border of the fused hyo-hypoplastral plate. This anterior plastral valve is moved upward by the contraction of the specially developed muscle — the *nucho-plastralis* (Hasan, 1941), described as the *trapezius* by George and Shah (1955). This muscle arises from the nuchal plate, runs along the base of the neck, and is inserted on the epiplastral plate. When the *trapezius* (=*nucho-plastralis*) muscles contract the anterior plastral lobe is lifted upward to close the shell. In addition, other muscles are also taking part in the closing mechanism of the anterior plastral lobe; these are: the clavicular part of the *deltoideus,* the *rectus capitis cervico-plastralis,* and the part of the *pectoralis* muscle which has its origin on the movable part of the plastron. The skin connecting the legs and the plastron also exerts some pull after the legs are retracted under the shell. The *trapezius* muscle is found only in the Trionychidae. Thus, though the anterior plastral lobe cannot be completely closed in *Trionyx gangeticus,* to a certain extent it can be lifted up to protect the retracted head, neck and fore limb. In this animal, as in the Cyclanorbinae, the *trapezius* muscle is present and works in a fashion similar to that in *Lissemys* (George and Shah 1955).

The infracaudal valve in all the members of the subfamily Cyclanorbinae is a small posterior part of the plastron which is demarcated by a transverse groove and which lies behind the xiphiplastral plates. Here also there is no regular hinged condition. Part of the *flexor caudae superficialis* muscle described for the closing mechanism of the supracaudal valve in the carapace of these animals is used for moving the infracaudal valve upward. Thus, when this muscle contracts the supracaudal as well as the

infracaudal valves are moved in opposite directions towards each other to close the shell posteriorly.

For the protection of the hind limbs in these animals an extra pair of cutaneous flaps is developed. These are known as the femoral valves. Each femoral valve is more or less hinged with the side of the xiphiplastral plates and is capable of valvular movements. The closure of the femoral valves is brought about when the ligament connecting the shank of the leg and the valve is tensed, as the legs are retracted under the shell. The skin connecting the legs and the valves also exerts some pull on the valves when the skin is drawn in as the legs are pulled under the shell.

Finally, it may be said that some chelonians have developed certain features like movable plastral or carapace parts by which they can close themselves in a box to protect their soft parts. Besides this, wherever the posterior plastral lobe or the posterior part of the carapace is movable, this capacity for movement also serves to facilitate the egg-laying process by widening the gap between the carapace and the plastron.

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ABBREVIATIONS

At.P.	Attrahens pelvium
At.P.′	Area of origin of attrahens pelvium
Car.	Carapace
C.Carp.	The position of the posterior hinged part of carapace in *Kinixys* when shell is completely closed
C.Dl.	Clavicular part of deltoideus
C.Dl.′	Area of origin of clavicular deltoideus
C.S.Isc.	Cut surface of ischium
C.S.Isc.′	Area of cut surface of ischium where it is fused with plastron
C.S.P.Isc.	Cut surface of pubo-ischial joint which is fused with plastron
C.S.P.Isc.′	Area of pubo-ischial attachment on plastron
F.C.S.	Part of flexor caudae superficialis
F.C.S.′	Area of insertion of F.C.S. on plastron
F.V.	Femoral valve
H.A.P.	Hinged joint of the posterior plastral lobe
H.A.P.′	Place of valvular movement of the anterior plastral lobe in *Lissemys*
H.P.P.	Hinged joint of the posterior plastral lobe
H.P.P.′	Place of valvular movement of the subcaudal valve of plastron in *Lissemys*
J.Car.	Hinged joint in carapace in *Kinixys*
P.	Pectoralis
P.′	Area of origin of pectoralis
P.C.Ca.	Precoracoid cartilage
P.G.	Pelvic girdle
P.G.′	Shifted position of pelvic girdle in *Kinixys* when the shell is completely closed

Pl.	Plastron
R.Carp.	The position of the posterior hinged part of the carapace in *Kinixys* when the shell is fully opened
R.C.C.	Retrahens capitis collique
R.C.C.P.	Rectus capitis cervico-plastralis
R.C.C.P.′	Area of origin of rectus capitis cervico-plastralis
Rt.P.	Retrahens pelvium
Rt.P.′	Area of origin of retrahens pelvium
S.Dl.	Scapular part of deltoideus
Sk.C.	Skin connection between the two hinged parts of the carapace of *Kinixys*
Tn.	Tendons connecting cervical vertebrae with plastron
Tn.′	Place of insertion of the tendons on the plastron
Tr.	Trapezius
Tr.′	Area of insertion of trapezius

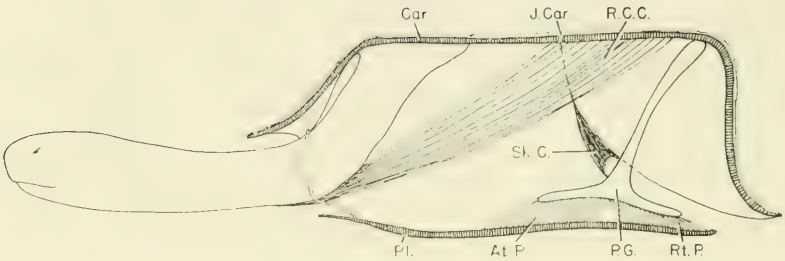

Fig. 1. *Kinixys erosa:* Side view showing extended neck and the position of the muscles, the hinged posterior part of carapace and the pelvic girdle when the shell is open.

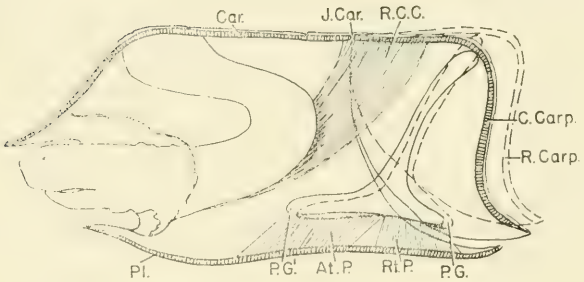

Fig. 2. *Kinixys erosa:* Side view showing the retracted head and neck, the contracted muscles and the shifted position of the pelvic girdle when the shell is closed.

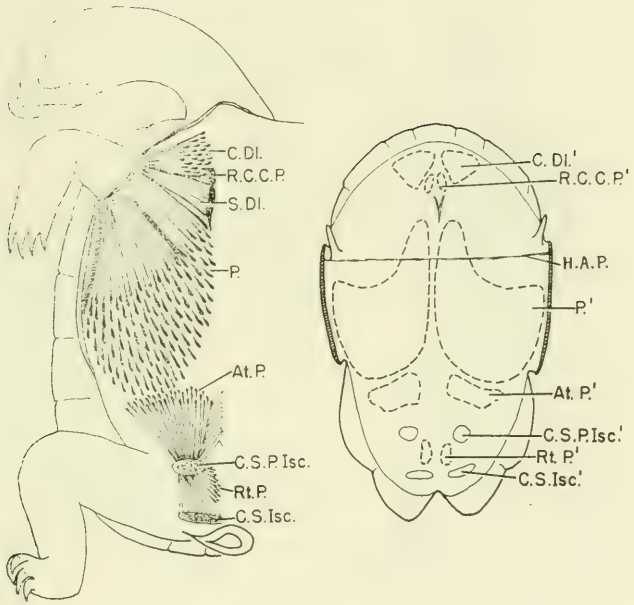

Fig. 3. *Pelusios subniger: Left,* the superficial ventral muscles in the shell region exposed. *Right,* the inner surface of the plastron showing the area of origin of various muscles.

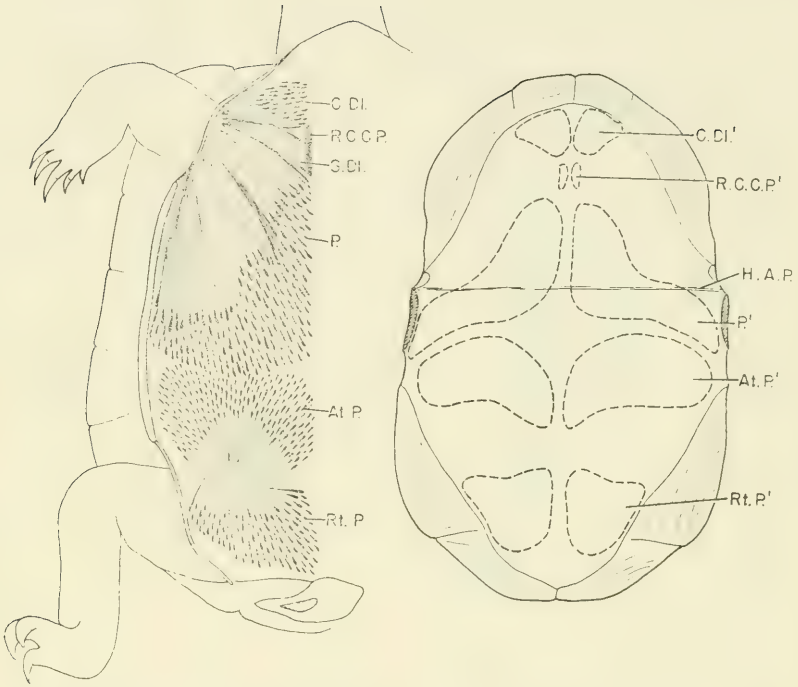

Fig. 4. *Terrapene carolina carolina: Left,* the superficial ventral muscles in the shell region exposed. *Right,* the inner surface of the plastron showing the area of origin of various muscles.

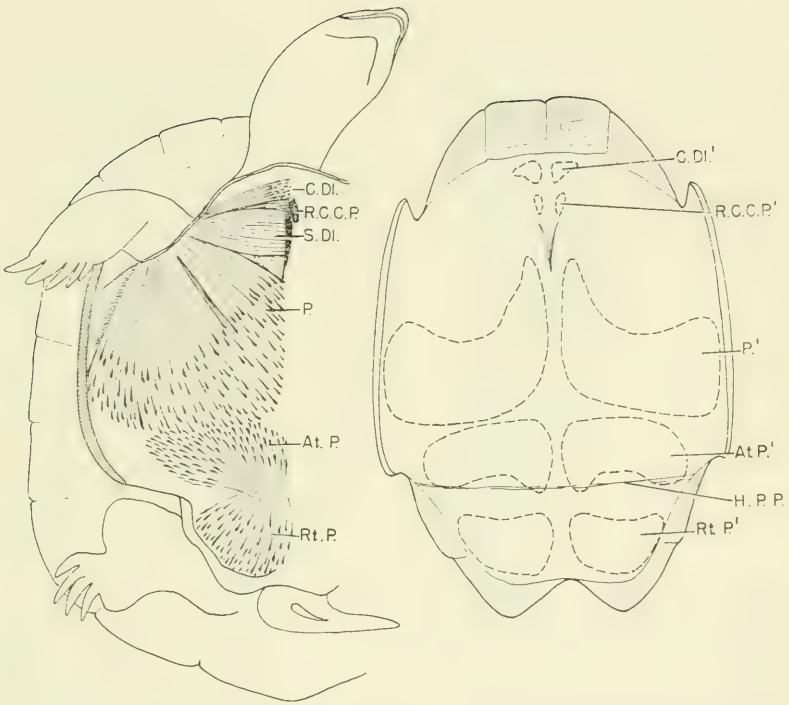

Fig. 5. *Testudo hermanni: Left,* the superficial muscles in the shell region exposed. *Right,* the inner surface of the plastron showing the area of origin of the various muscles.

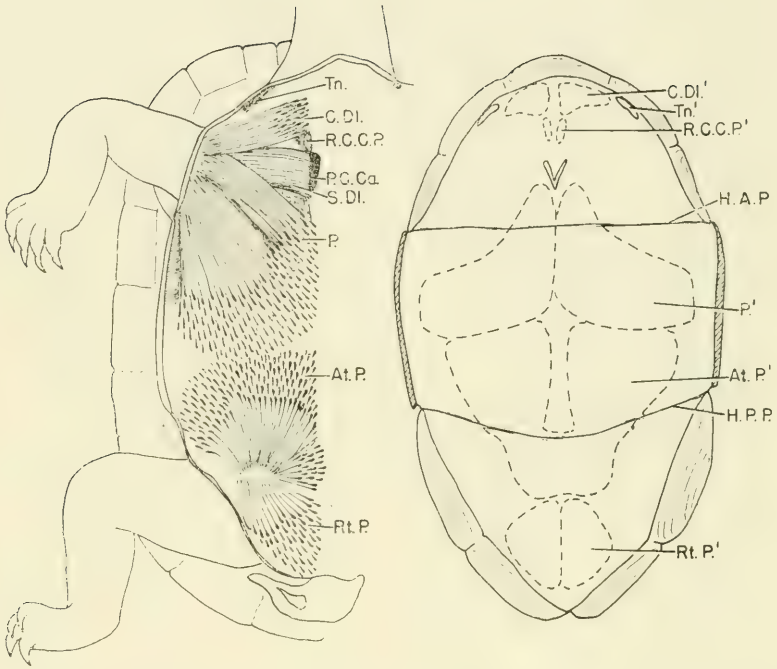

Fig. 6. *Sternotherus carinatus minor: Left,* the superficial ventral muscles in the shell region exposed. *Right,* the inner surface of the plastron showing the area of origin of various muscles.

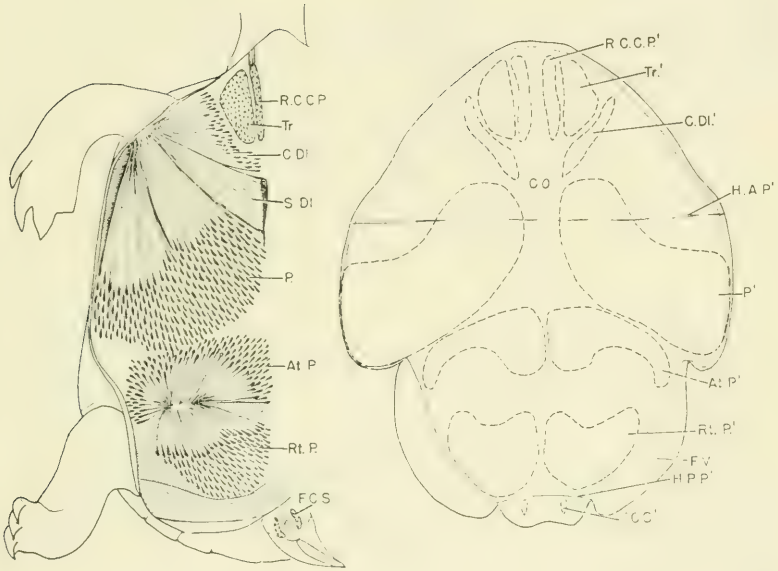

Fig. 7. *Lissemys punctata: Left,* superficial ventral muscles in the shell region exposed. *Right,* the inner surface of the plastron showing the area of origin of various muscles.

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. DECEMBER 30, 1960 NUMBER 131

A SECOND RECORD OF THE FOSSIL RODENT *PALUSTRIMUS* WOOD

By CRAIG C. BLACK

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In July of 1959, while working in the Goshen Hole area in eastern Wyoming, Laura McGrew took Sabra B. Black and me to a microfaunal locality about six miles west northwest of Fort Laramie National Monument, just south of the North Platte River. A small surface sample of isolated teeth and about twenty pounds of fine, gray channel sand were collected at that time.

The following genera have been recognized in the assemblage to date: *Prosciurus, Promylagaulus, Heliscomys, Palustrimus,* and *Palaeocastor.* The presence of *Heliscomys* and especially *Prosciurus* would indicate an early Miocene age. Until recently *Prosciurus* was not known to occur after the late Oligocene, but it has now been recorded from a new basal Miocene formation in South Dakota (Macdonald, personal communication). Its presence in this assemblage together with the definitely early Miocene *Promylagaulus* and *Palustrimus* would lead me to believe that the fauna is lowermost Miocene. A detailed report on this fauna is deferred in the hope that a larger sample can be secured in the near future. The purpose of the present note is to call attention to this new early Miocene locality and to record the presence of *Palustrimus* in the assemblage.

Palustrimus was described by Wood in 1935, from a single tooth, LM^1, in the Yale Peabody Museum collections from the Upper John Day. The present specimen represents the second record for the genus and corroborates Wood's original determination. This occurrence is doubly important since the type of *Palustrimus lewisi*, Y.P.M. No. 10572, cannot be found in the Yale collections. There is a note with the label for the specimen which states that it has been lost since 1950.

I take this opportunity to thank Laura McGrew for showing us the locality, and Dr. J. T. Gregory for allowing me free access to the John Day rodent collections then in his care. The drawing is by Mr. James O. Farley and was made possible by a grant from the Gulf Oil Corporation.

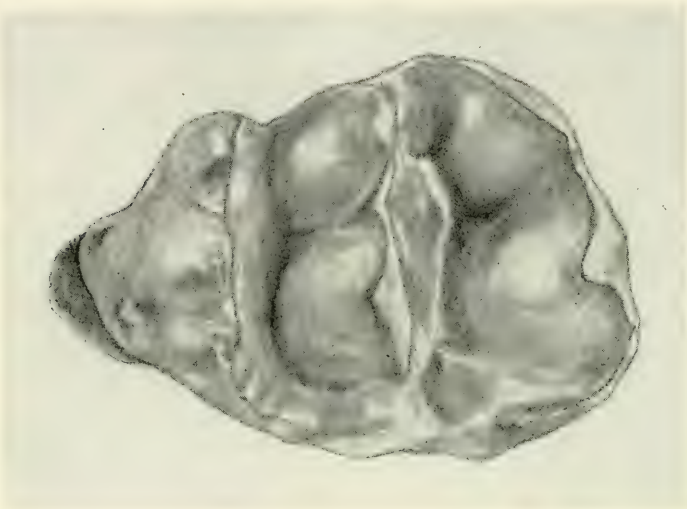

Figure 1. *Palustrimus* sp., LM^1, X30.

Abbreviations used:

Y.P.M. — Peabody Museum of Natural History, Yale University

M.C.Z. — Museum of Comparative Zoology, Harvard University

Order RODENTIA

Family MURIDAE

PALUSTRIMUS sp.

Referred Specimen. M.C.Z. No. 7353, LM^1.

Horizon and *Locality.* Lower Miocene. S. 15, T. 26 N., R. 65 W., Goshen County, Wyoming.

Description. The tooth is composed of three transverse lophs joined lingually by a high ridge. The valleys between the three

lophs are extremely deep and pass directly across the tooth to the lingual ridge. Each loph is composed of three cusps, the central cusp in each case being dominant and the marginal ones lower. The lingual cusps of each loph are joined together by the lingual ridge, which carries several smaller cuspules along its length. The lophs increase in width from front to back, giving the tooth a triangular appearance. The transverse valleys are much deeper than the notches between the cusps. The notch between the buccal and central cusps is quite deep on the anterior loph, shallower on the central loph and almost completely absent on the posterior loph. There is a small accessory cusp rising from the floor of the posterior transverse valley just in front of the shallow notch between the buccal and central cusp of the last loph. The first and second crests are slightly convex anteriorly, while the last crest is slightly concave anteriorly.

The measurements (in mm.) are: anteroposterior, 2.45; width anterior loph, 1.35; median loph, 1.60; posterior loph, 1.77.

Discussion. There is little doubt that this specimen is congeneric with *Palustrimus*. That it is conspecific with *P. lewisi* seems highly doubtful, however, but the present material does not warrant the erection of a new species. It differs from *P. lewisi* in the possession of a high, lingual ridge connecting the transverse lophs and bearing several accessory cuspules and in having convex rather than concave anterior and median lophs. In other respects the tooth is extremely similar to that of *P. lewisi*. Both have the three transverse crests composed of three cusps each.

Unfortunately, until more material of this peculiar genus is known its taxonomic position cannot be definitely determined. It is like nothing else known among the rodents from the North American Tertiary. Wood's (*op. cit.*) assignment of the genus to the Muridae would seem to be the most likely one at present, although the possibility of a geomyoid relationship (Wilson, 1949, p. 126) should not be overlooked.

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BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. DECEMBER 30, 1960 NUMBER 132

THE STATUS OF *SPHAERODACTYLUS PICTUS*, WITH COMMENTS ON THE DISTRIBUTION OF *S. SPUTATOR* AND *S. SABANUS*

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Garman (1887:20), in his description of *Sphaerodactylus pictus*, lists its range as the island of St. Christopher's (= St. Kitts), West Indies. Barbour, in his monograph of the genus (1921:263) and in his first checklist of Antillean amphibians and reptiles (1930:85) lists the range as St. Kitts. In his second (1935:104) and third (1937:115) Antillean checklists, Barbour includes the island of Nevis in the range of *pictus*, and states that it (*pictus*) is possibly a synonym of *S. sputator*.

In his monograph, Barbour (1921:226) separates *pictus* from *sputator* on the degree to which the dorsal scales are keeled (rather weakly in *pictus*, and strongly in *sputator*), and on the number of dorsal scales equal to the distance from the tip of the snout to the center of the eye (9 in *pictus*, and 10 in *sputator*). Examination of the types of *pictus* (MCZ 6071) from St. Kitts, and of a large series of *sputator* (MCZ 16598—16633, 16635—16641) from St. Eustatius (= Statia) indicates that the first of the two characters used by Barbour to separate these species is extremely subjective and of doubtful value. The second character, which involves allometric growth of the head and dorsal scales, varies from 7 to 10 scales in *sputator*. The number of dorsal scales in the "standard distance" of *pictus* is thus included. Further examination reveals no character of scutellation which will separate the two forms.

Garman (1887:20) describes the color and pattern of *pictus* as:

> "Greyish with three or four rows of brown spots on each side. On the snout there is a brown band from each eye around the end; a median band meets these on the rostral. Behind the eyes, on the head, there are six longitudinal bands of brown, four of which join to form two on the occiput, and these meet the laterals on the neck forming two which are continued above the shoulders. A light line across the forehead from one orbit to the other. Two or three light streaks, across the back of the head and neck, appear in some. On a very young one there are five narrow, transverse, dark-edged streaks of white between the eyes and the base of the tail. There are traces of brown blotches on the lower surface."

A series of *sputator* in the Museum of Comparative Zoology indicates that the juvenile pattern of this species consists of white crossbands, with dark brown edges, on the neck, trunk, and tail. There are 5 to 8 of these crossbands between the level of the eyes and the base of the tail. The crossbands alternate with areas of dull brown ground color. The adult has a pattern of 2 to 3 white crossbands, usually with dark brown edges, on the neck and shoulders. The white markings on the trunk are always edged, at least in part, with dark brown. The pattern may be in the form of crossbands, or may be broken into wavy lines or spots. The white markings may fade to a light tan. In a few individuals the dark brown edge of the dorsal spots tends to form longitudinal rows or stripes on the light ground color. Both juveniles and adults have a dark brown stripe on the canthus rostralis, and a white stripe connecting the orbits across the top of the head. From the above description it is evident that the variation which occurs in the color pattern of *sputator* includes the pattern thought to be characteristic of *pictus* (see Fig. 1).

Since their scutellation and patterns are identical, *Sphaerodactylus pictus* Garman should be considered a synonym of *Sphaerodactylus sputator* (Sparrman), and the range of *sputator* should be extended to include the island of St. Kitts.

A confusing factor in establishing the status of *S. sputator* is Barbour's reference (1923:2) to its color pattern. He states that *sputator* is:

> ". . . One of the dichromatic forms, as are so many of the large-scaled species — and perhaps others as yet

Figure 1. Variation in the trunk markings of adult *Sphaerodactylus sputator* (relative size and position is diagrammatic for ease of comparison). A and F (MCZ 16619 and 16611, respectively) are from the island of Statia; B (UF 10039-2) is from St. Martin; C (UF 10038), D and E (MCZ 6071) are from St. Kitts. D and E are cotypes of the synonym, *pictus*.

> little known. The types are females evidently. The males are much smaller than the females, uniform greyish brown through life, or at the most with a few fine scattered dots usually on the head. The females are large, bulky and with a great variety of broken bands, blotches and spots of varying size."

Although Barbour does not list the catalogue numbers of the specimens he refers to in this paper, he does state that they were collected on Statia in 1922 by James L. Peters. This series is MCZ 16598—16633, 16635—16641. At the time of his writing, this series contained both *S. sputator* and *S. sabanus*. This is evident in Barbour's reference to the large "females" (= *sputator*) with blotches, bands and spots, and to the small "males" (= *sabanus*) of a uniform brown.[1] Examination of the present series of *sputator* shows little or no sexual dichromatism, and the snout-vent length of the males (31-35 mm., with a mean of 32.8) is slightly greater than that of the females (28-35 mm., with a mean of 31.7).

On 10 July 1958, Dr. Walter Auffenberg and I collected an adult specimen of *S. sputator* in Basseterre, St. Kitts, thereby confirming the existence of this species at the type locality of the synonym, *pictus*. On 15 July 1958, we collected two adult *sputator* on St. Martin, 2½ miles west, and ¼ mile north of Philipsburg, near Devil's Hole.

The range of *S. sputator*, as indicated by the specimens available to me at this time, includes the islands of Statia (MCZ 16598—16633, 16635—16641 (29); UMMZ 57010), St. Kitts (MCZ 6071 (3); UF 10038), and St. Martin (UF 10039 (2); PWH 474A, 606 (5)). Future collecting will probably establish its existence on Nevis and Saba, the two remaining islands of the Saba to Nevis chain of islands.

The range of *S. sabanus* includes all of the islands of the Saba to Nevis chain of islands. It is found on Saba (MCZ 45215—45217; USNM 103985—103993, 103995—104003), Statia (MCZ 54010—54015 (158)), St. Kitts (UF 10041 (9), 10042 (9), 10043 (9), 10044 (9), 10045 (10); PWH 422; UMMZ 83317), and Nevis (UF 10040 (3); PWH 414; UMMZ 83316 (2); MCZ

[1] The *sabanus* were later separated from the series and recatalogued under the name *elegantulus* as MCZ 54010 - 54015. That they are not *elegantulus* is now clear since in addition to other features there is no crossbanding in the juveniles of this series. Cochran (1938) pointed out that the juveniles of *sabanus* are unmarked like the adults, while Barbour (1921) described the crossbanded juveniles of *elegantulus*. This confusion of *elegantulus* and *sabanus* is not significant for the present paper; a study of these and other Lesser Antillean sphaerodactyls, including a redefinition of all the species, is in preparation and will be presented later.

38374). Barbour's record of *pictus* (= *sputator*) on Nevis (1935:104 and 1937:115) seems to be based on the Museum of Comparative Zoology specimens of *sabanus* listed above.

The fieldwork during the summer of 1958 was supported by National Science Foundation Grant G-3896 and the Florida State Museum. Specimens collected on this trip have been placed in the University of Florida Collections, Gainesville (= UF). I would like to thank Dr. Ernest Williams (Museum of Comparative Zoology, Harvard = MCZ), Dr. Doris Cochran (U. S. National Museum, Washington = USNM), Dr. Norman Hartweg (University of Michigan Museum of Zoology, Ann Arbor = UMMZ) and Dr. P. Wagenaar Hummelinck (Der Rijks-Universiteit Zoölogisch Laboratorium, Utrecht = PWH) for the loan of specimens in their care, and Dr. Walter Auffenberg, Dr. William Riemer, Andrew Arata, and Charles Myers for their criticism and interest.

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BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. FEBRUARY 27, 1961 NUMBER 133

ON THE GENERIC LIMITS IN THE FAMILY PILIDAE (PROSOBRANCHIA: MOLLUSCA)[1]

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I

Members of the molluscan family Pilidae have been known to science since pre-Linnaean times. Although the family has been defined, the generic limits — and particularly generic relationships — require further clarification. Morphologic investigations have been conducted on representatives of individual species, but only rarely have these studies been of a comparative nature. An attempt has been made in the present paper to review and collate the available information upon which generic limits may be established. Studies on the comparative morphology of the kidney and the penial complex are also presented.

In the following discussion the family Pilidae will be considered to consist of seven genera. Included in the genera *Pila*, *Lanistes*, *Afropomus*, and *Saulea* are the Old World species; members of *Pomacea*, *Marisa*, and *Asolene* constitute the New World species. These genera have been erected primarily upon conchological characteristics based on such criteria as color, size and shape of the shell, types of sculpturing (if present), and the presence or absence of an umbilicus.

II

Attempts have been made by others to divide the family into two major groups, the Old and New World forms, on the presence or absence of a calcareous operculum. Newer knowledge

[1] This study was supported (in part) by a research grant (E-513-C) and a training grant (2E-46) from the National Institutes of Allergy and Infectious Diseases, National Institutes of Health, Public Health Service.

has shown that this criterion is unsound, since only *Pila* has a calcareous operculum. However, the phylogenetic significance of the operculum even in *Pila* is limited since calcification is a secondary process which occurs after the snail hatches (Ranjah, 1942).

The longisiphonate or brevisiphonate nature of the respiratory siphon has also been used as a criterion for the separation of Old and New World species, and appears to have some validity. *Pila* and *Lanistes* are brevisiphonate, and the present study indicates that the siphon of *Afropomus* is similar. *Saulea* can only tentatively be accepted as a valid genus since no description of its anatomy exists. The New World genera, *Pomacea* and *Marisa*, are longisiphonate; however, *Asolene* has been reported (Scott, 1943) to have an aberrant siphon (brevisiphonate ?), and may be closely related to the Old World genera. It has been suggested that the morphology of the siphon is not of phylogenetic significance, but reflects an adaptation to ecological conditions (Prashad, 1925).

The radulae of the Pilidae are all taenioglossate and have the formula 2:1:1:1:2. Intra-specific variations, however, reduce the value of radular morphology at levels below the family. The genus *Turbinicola* was erected on the basis of radular morphology (Annandale and Prashad, 1921; Prashad, 1931); however, Pilsbry and Bequaert (1927) consider this group to be no more than a subgenus of *Pila*.

The eggs of the various species provide several promising and characteristic differences which may aid in arriving at taxonomic limits of the genera. Lipochromes, which color the eggs or egg shells, occur in species of *Pomacea*, but are absent in the eggs of *Pila* and *Lanistes* (Comfort, 1947). Eggs of *Marisa cornuarietis* are peculiar in possessing an orange pigment when first deposited, but this soon disappears (Michelson, 1956).

The presence of an egg-shell is biologically significant and may be of phylogenetic importance. Both *Pila* and *Pomacea* produce such eggs, and in both cases the eggs are deposited out of water. *Marisa* is completely aquatic and its eggs are gelatinous. Eggs of *Lanistes* were initially reported as membranous by D'Ailly (Pilsbry and Bequaert, 1927), but recent observations have demonstrated that they are gelatinous and are deposited below the water-line (McMahon et al., 1957). Information concerning the eggs of *Asolene* is limited to a report by von Ihering (*vide* Pilsbry, 1933) in which it is stated that the eggs are gelatinous. The eggs of *Saulea* and *Afropomus* have not been described.

III

The soft parts of 8 species of Pilidae (representing the genera *Pila*, *Lanistes*, *Afropomus*, *Pomacea*, and *Marisa*) were examined for characteristic anatomical differences. Only two structures, the kidney and the penial complex, appeared promising in this respect.

The identity and sources of the material used in this study are presented in Table 1. Specimens of *Pila, Lanistes, Afropomus,* and the South American *Pomacea* were obtained from the collections of the Museum of Comparative Zoology, Harvard University, through the courtesy of Dr. William J. Clench. These specimens were fixed either in Bouin's solution or 70% ethyl alcohol and subsequently stored in 70% alcohol. Specimens of *Marisa* and *Pomacea paludosa* obtained from laboratory colonies were first relaxed in boiled water and subsequently fixed in Bouin's, Zenker's, or Newcomer's solution. Since not all specimens were fixed in the same way only gross and micro-anatomical features were studied. For micro-anatomical study, tissues were embedded in paraffin, sectioned at 9-12.5μ, and stained with Lillie-Mayer hemalum and eosin. A total of 82 snails were examined including at least 5 specimens of each species.

A. *The Kidney.* The kidney of members of the Pilidae is composed of two distinct regions, an anterior and a posterior chamber. The anterior chamber is a discrete tubular structure that partially extends into the mantle cavity opening into it through an excretory pore. The posterior chamber is embedded in its entirety in the visceral mass. This chamber is not compact, but consists of a large vacuolated area surrounded laterally and ventrally by a thin, transparent membrane, and bounded dorsally by a large shield-like mass of tissue. The posterior chamber is further limited anteriorly by the pericardial membrane, although access to the pericardium is provided by the renopericardial pore. Descriptions of the kidney of specimens representing the various genera follow:

Pila. In *P. globosa* (Fig. 1E) the dorsal surface of the posterior chamber is broadly rectangular and measures approximately 1.8-2.0 times the length of the anterior chamber. The dorsal surface is brown and blood vessels are not prominent. The anterior chamber is triangular and is so oriented that its main axis is continuous with the axis of the posterior chamber. The kidney in the species from Siam was morphologically similar.

Lanistes. In *L. boltancanus* (Fig. 1 C) the dorsal surface of the posterior chamber differs from that of *Pila* in being broader anteriorly. The ratio of the length of the posterior chamber to the anterior chamber is approximately 0.8 :1 to 1.1. The anterior chamber is considerably longer than in *Pila* and is triangular in shape. The main axis of the anterior chamber in *Lanistes* is also oriented so that it is continuous with the axis of the posterior chamber.

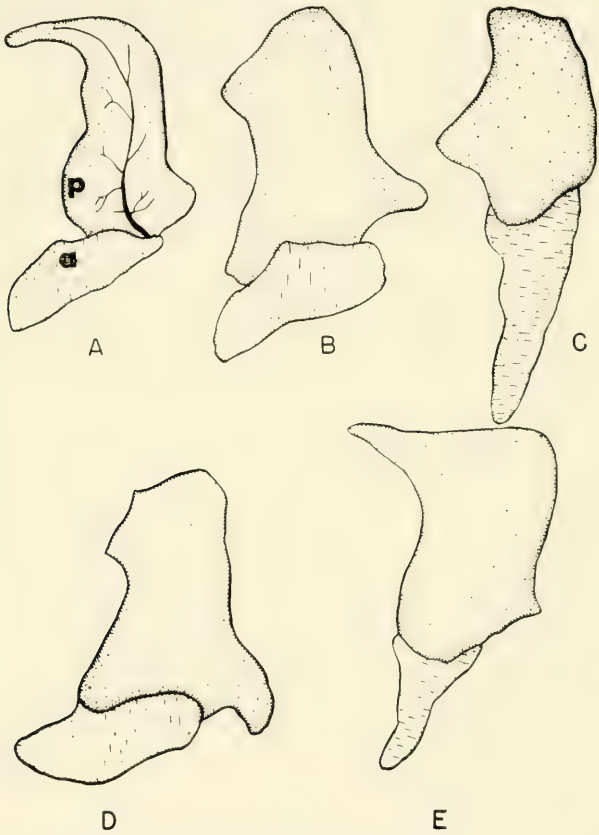


Figure 1. Semi-diagrammatic sketch of the dorsal surface of the kidney in five species of Pilidae: (A) *Afropomus balanoideus,* (B) *Pomacea paludosa,* (C) *Lanistes boltaneanus,* (D) *Marisa cornuarietis,* (E) *Pila globosa.* The posterior chamber (*p*) and the anterior chamber (*a*) of each kidney illustrated are oriented as in Figure 1A.

Afropomus. The kidney in *A. balanoideus* (Fig. 1 A) differs most radically from those of the other genera. The posterior chamber is distinctly triangular in shape and its apex is reflected to the right. Furthermore, it is the only form in which blood vessels are prominent on the dorsal surface of the kidney. The anterior chamber is irregularly rectangular in shape, and its axis lies at an obtuse angle to that of the posterior chamber.

Pomacea. The morphology of the kidney was similar in the four species examined. In *P. paludosa* (Fig. 1 B), the posterior chamber is broadly rectangular and has a prominent protuberance situated anteriorly on its left margin. The anterior chamber is irregular in shape and its long axis lies at an obtuse angle to the axis of the posterior chamber.

Marisa. The kidney of *M. cornuarietis* (Fig. 1 D) is very similar to that found in species of *Pomacea*, thus further strengthening the suggestion that *Marisa* should be considered a subgenus of *Pomacea* (Baker, 1930; Pain, 1950). The lateral protuberance of the posterior chamber in *Marisa* is larger and farther anterior than in *Pomacea.* In addition, the posterior chamber surrounds the anterior chamber more completely in *Marisa* than in *Pomacea*

B. *The Penial Complex.* The penial complex in the members of the Pilidae arises from the mantle as a finger-like projection. It consists primarily of a large outer penial sheath which enfolds the true penis. Since there is no direct connection between the penis and the vas deferens, sperm must be transmitted from the latter organ to the former, and thence to the female. Sachwatkin (1920) first described the presence of an internal sperm canal in the penis of *Ampullaria gigas.* Prashad (1925), however, found that in *Pila globosa* an external sperm canal was present. Our study indicates that both workers were correct and that an internal canal is characteristic of the New World species and an external canal characteristic of the Old World species (Figs. 2-4).

IV

Although additional studies will be needed to establish the generic limits in the family Pilidae, there appears now to be sufficient information to separate the Old from the New World genera, as shown in Table 2.

It is apparent from the foregoing that sufficient data are not available to permit a critical interpretation of the phylogenetic relationships within the family. Nevertheless, there appears to be an evolutionary trend towards the establishment of the family in the terrestrial biotope. The presence of a respiratory sac, in addition to gills, suggests a morphological adaptation for the transition from the aquatic to the terrestrial habitat. Species in two genera (*Pila* and *Pomacea*) are highly amphibious and even deposit their egg masses out of water; the presence of a calcareous egg shell further reduces the dependence of *Pila* and *Pomacea* on an aquatic habitat. If the premise is accepted that the family Pilidae is evolving towards a terrestrial mode of life, then we must conclude that both *Pila* and *Pomacea* represent evolutionary advances in that direction.

TABLE 1

The Specific Identity, Origin, and Number of Specimens Examined

Species	Origin	No. Specimens Examined
Pila globosa Swainson	Calcutta, India.	7
	Bangkok, Thailand	5
Lanistes boltancanus (Röding)	Cairo, Egypt	10
Afropomus balanoideus (Gould)	Liberia	8
Marisa cornuarietis (Linné)	Rio Piedras, Puerto Rico	15
Pomacea paludosa Say	Miami, Florida	12
Pomacea interrupta Sowerby	Chonta anticline, Peru	10
Pomacea columellaris Reeve	Huanuco, Peru	10
Pomacea nublia Reeve	Huanuco, Peru	5

TABLE 2A

Diagnostic Characteristics of the Major Genera of the Family Pilidae [1]

Genus	Shape of Shell	Operculum	Respiratory Siphon	Sperm Canal
Pila	Dextral; sub-ovate to globose	Calcareous	Brevisiphonate	External
Lanistes	Sinistral; sub-ovate, turbinate, or carinate	Corneous	Brevisiphonate	External
Afropomus	Dextral; globose	Corneous	Brevisiphonate	External
Saulea	Dextral; sub-ovate	Corneous	?	?
Pomacea	Dextral; sub-ovate, ovate, or globose	Corneous	Longisiphonate	Internal
Marisa	Dextral; secondarily planorboid	Corneous	Longisiphonate	Internal
Asolene	Dextral; sub-ovate, ovate, or neritoid	Corneous	Longisiphonate	?

[1] The morphological characteristics of the kidney of each genus are presented

TABLE 2B

Diagnostic Characteristics of the major Genera of the Family Pilidae [1]

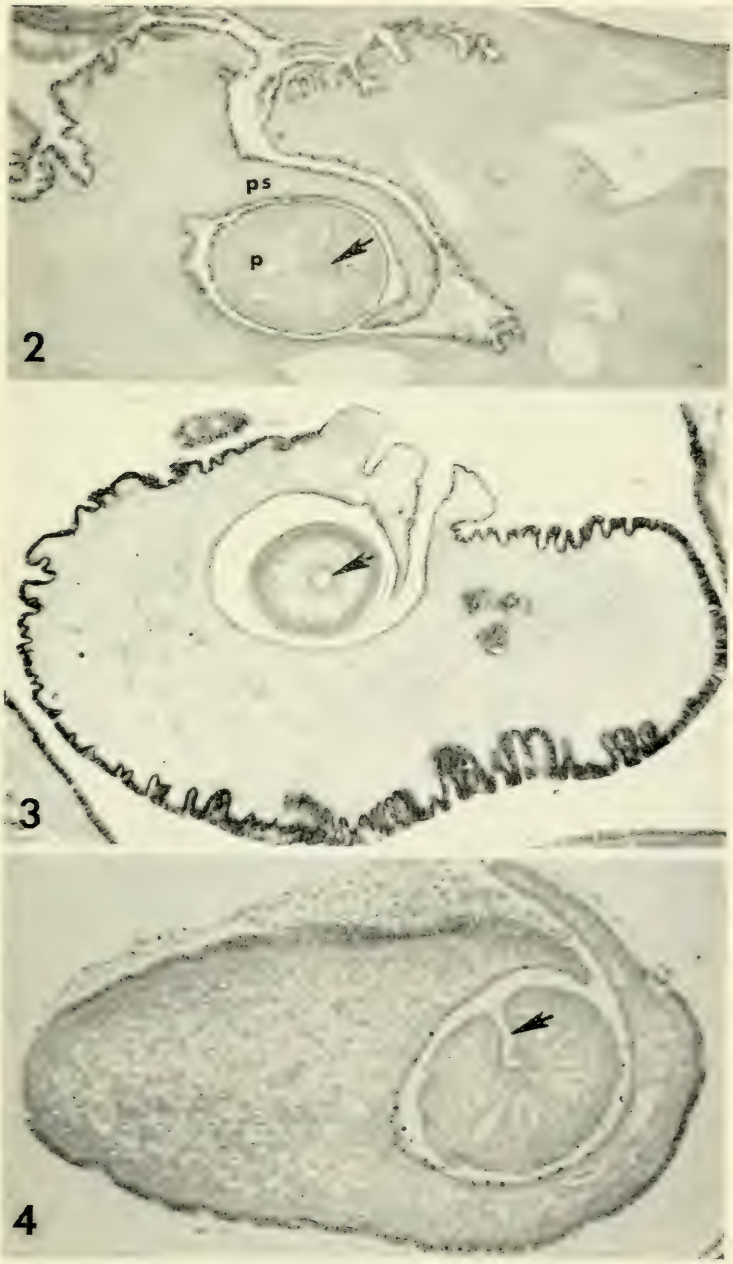
Genus	Nature of Eggs	Oviposition Site	Behavior	Geographical Distribution
Pila	Calcareous shell; non-pigmented	In banks or mudflats near water	Highly amphibious	Africa and Asia
Lanistes	Lacking shell; gelatinous; non-pigmented	On submerged vegetation, etc.	Aquatic or slightly amphibious	Africa
Afropomus	?	?	?	Africa
Saulea	?	?	?	Africa
Pomacea	Calcareous shell; pigmented	On emergent parts of aquatic vegetation	Moderately amphibious	South America; Central America; West Indies Southern U.S.
Marisa	Lacking shell; gelatinous and pigmented when first deposited	On submerged vegetation, etc.	Aquatic	South America; West Indies
Asolene	Lacking shell; gelatinous; pigmented (?)	On submerged vegetation, etc.	? Aquatic	South America

[1] The morphological characteristics of the kidney of each genus are presented in Fig. 1.

Figure 2. Cross-section through the penial sheath (*ps*) and penis (*p*) of a specimen of *Pomacea paludosa*. The location of the internal sperm canal is indicated by the arrow. The anatomy of the penis demonstrated in this figure is similar to that observed in all species of *Pomacea* examined. Hemalum and eosin, X47.

Figure 3. Cross-section through the penial sheath and penis of a specimen of *Marisa cornuarietis*. The arrow points to the internal sperm canal. Hemalum and eosin, X29.

Figure 4. Cross-section through the penial sheath and penis of a specimen of *Lanistes boltaneanus*. The arrow points to the external sperm canal. A similar type of sperm canal was found in the penes of specimens of *Pila globosa* and *Afropomus balanoideus*. Hemalum and eosin, X43.


ps
p
2
3
4

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BREVIORA

Museum of Comparative Zoology

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ENZYMATIC CONSTITUTION OF *ALSOPHIS* SALIVA AND ITS BIOLOGICAL IMPLICATIONS

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I. Introduction

As long as fifty-eight years ago (Alcock and Rogers, 1902) it was noted that the saliva of certain ostensibly harmless colubrids had toxic properties. Recently, members of the genus *Alsophis* have been suspected to have a toxic saliva. A. S. Rand (MS.) has detailed accounts of *Alsophis portoricensis* feeding behavior and of the effects of bites in man. Neill (1954) relates an instance of toxic effects in himself from an *A. anguilifer* bite.

The purpose of this paper is two fold: 1) to attempt to provide enzymatic confirmation for the tentative conclusion that the colubrid *Alsophis portoricensis* has a truly active salivary secretion (i.e. with venomous properties); and 2) to characterize the activity found in terms of similar enzymes represented in another colubrid and in a crotalid, thus providing a comparative basis for evaluation of the biological implications of this activity.

Natrix sipedon from Florida and *Crotalus atrox* from Texas provided the other preparations. Commercial crystalline *Crotalus* venom was made available by Dr. W. R. Sistrom. The *Natrix* and *Alsophis* preparations were collected by a straightforward method in the laboratory.

II. Collection of Saliva

A small tablet of washed, fine-pore cellulose sponge, previously moistened with distilled water, was inserted in the reptile's mouth with stainless steel forceps. *Alsophis* readily grasped and chewed on the sponge, but with *Natrix* swabbing was necessary.

When relinquished, the sponge was squeezed and rinsed into a tared weighing bottle. The bottle was placed in a chilled desiccator and evacuated until dry over potassium hydroxide at 5°C. This procedure was repeated over the course of several weeks until a quantity deemed sufficient for subsequent tests was collected.

Ten "milkings" coming from two individuals provided 22 milligrams of *Alsophis* preparation over a period of three weeks. Six *Natrix*, each milked once on four occasions equally spaced over the same three weeks, gave a total of 26 milligrams of preparation.

III. Estimation of protein content

Since all known enzymes are proteins, the first step in gaining a fair comparison of activities depends on the total protein content of the saliva. This was estimated for small redissolved duplicate samples of preparation by the Folin-Lowry method (Lowry et al., 1951). Bovine serum albumin was adopted as the reference protein standard. Protein by percent weight for the three preparations is given below (Table 1).

TABLE 1

Preparation	% protein (± 2%)
Alsophis	43.0
Crotalus	99.5
Natrix	16.5

Alsophis is here seen to lie between the harmless colubrid and overtly venomous crotalid with respect to potentially active protein content. These results were used to adjust the dissolved preparations used in the later experiments to equivalent protein content.

IV. Spreading factor estimation

The reports of Neill and Rand (above) indicate the presence of a "spreading factor," seen in many natural venoms (Kellaway, 1939). In the case of snake venoms this is probably a complex mixture of proinvasins and hyaluronidase (Zeller, 1948). These enzymes respectively inhibit destruction of the hydrolytic agent of the venom and destroy the mucoid structural material of the cell lattice by a hydrolytic action. The resultant loosening of the matrix favors the passive transport of the venom components of the tissue.

The method followed here has been modified from Fanilli and McClean (1939). It has the disadvantage that specificity is lost and the results are ill-defined. It is well suited to demonstrating low activities however.

Two dilutions of the preparation in question, adjusted to equal protein content, were mixed with equal parts of india ink and 0.9 saline. Of each dilution 0.025 ml. was injected intradermally on the shaved back of an etherized rat. Bovine serum albumin of approximately equal protein content was substituted for the saliva preparations in five otherwise similar control injections. Sites of injection were placed within the shaved area so that each was straddled by two controls. The diameter of each weal was read at one-half hour intervals. Since the progress of the spots was a nearly constant percentage of the original diameter for the first hour and one half, the observations below are for that range (Table 2). Rates fell off sharply after that period; the rate for *Crotalus* fell off sharply after the first half hour.

TABLE 2

	mgm preparation protein injected	% increase in diameter per hour (± 10%)
Crotalus	0.125	80
	0.068	55
Natrix	0.125	20
	0.063	0
Alsophis	0.130	50
	0.065	20
Controls 1	0.000	0
2	"	14
3	"	0
4	"	0
5	"	17

Again, according to this index, *Alsophis* shows a definite tendency toward "venomous" activity.

V. Proteinase

Another type of enzyme frequently active in venoms (Zeller, 1948) is proteinase. Work on the genus *Dromicus*, a relative of *Alsophis*, has demonstrated the activity of this enzyme type in extracts of the parotid gland (Donoso-Barros and Cardenas, 1959). Proteinases act hydrolytiely to reduce the chain length of proteins and large polypeptides, providing necrotic predigestion of the food object and destruction of the tissues. The fortuitous release of histamine from damaged and dissolved

tissue might be expected to enhance any neurotoxic activity in the venom too.

Proteolytic activity was estimated (Northrop et al., 1948) by measuring the residual material giving the Folin-Lowry reaction in an incubation mixture of enzyme and bovine serum albumin after precipitation with 0.1 molar trichloroacetic acid. Quantities of 0.25 mgm protein of preparation and 2.5 mgm of bovine serum albumin per milliliter were incubated in M/15 phosphate buffer at pH 7.2 and 37° C. Saliva preparations alone and albumin alone were also assayed for autogenous proteolysis; the added rates of release in these provided a subtractive correction for the incubation mixtures of preparation and protein.

Proteolysis rate is best taken over the first half hour where first order kinetics appear to obtain. The relative activities are given below, the average of two experiments.

TABLE 3

Preparation	μgm BSA hydrolyzed/ mgm preparation protein/ hour (± 2%)
Crotalus	28.3
Alsophis	12.3
Natrix	0.3

VI. Hemolysis

The lysis of red blood cells is a conspicuous part of the action of snake venoms (Kellaway, 1939). The major part of this effect is due to the action of phospholipase A on tissue phosphatides to produce lysolecithin. This substance renders erythrocytes extremely fragile (Zeller, 1948). The subsequent action of proteolytic enzymes results in the disruption of the cell wall (lysis). Other substances in venoms besides lipases promote lysis without first acting on an intermediate, and it is these which were measured here.

Following Bernheim (1947), aliquots of washed horse erythrocytes were incubated with measured quantities of the various preparations in buffered isotonic saline at 37° C. A blank was run to correct for autolysis in the buffered saline, and one aliquot was lysed by repeated freeze-thawing to give 100% lysis. At the end of the incubation period the cells were centrifuged down and the supernatant liquid was immediately read for absorbance at 579 mμ, an absorption peak of hemoglobin. This quantity when related to that of the completely lysed portion gave a

percentage lysis for the cells. Hemolysis rates are given below as percent lysis per ten micrograms preparation protein per milliliter per hour.

TABLE 4

Preparation	lysis/hour
Crotalus	4.42%
Alsophis	1.20%
Natrix	—0.73%

The negative value for the *Natrix* preparation indicates a lysis rate less than the control, i.e. a protective effect.

VII. Cholinesterase

The typical elapine venom, noted for neurotoxicity, is extremely high in a unique type of cholinesterase (Zeller, 1947). Presumably, since it is present in high concentrations, the curare-like effect of this venom is due to this enzyme's hydrolytic action on acetylcholine. This blocks transmission at neuromuscular junctions, and hence paralyzes the prey. However, inhibitors of this enzyme do not protect animals as fully as might be expected from the effects of cobra venom, including the neurotoxic effects (Zeller, 1948). The situation here is not as clear as might be hoped.

The assay method was essentially that of Hestrin (1949). The preparation was incubated with M/15 phosphate buffer at pH 7.2 and 30° C; acetylcholine concentration was four micromoles per milliliter. From the known protein content of the preparation and the measured disappearance of acetylcholine the activity of the preparation was established. Under the conditions described, accuracy was one tenth of a micromole. This was also the minimum amount of hydrolysis detectable.

TABLE 5

Preparation	Units esterase
Crotalus	0.0
Alsophis	0.2
Natrix	7.4

The unit of activity is conventionally defined as micromoles acetylcholine hydrolyzed per hour per milligram preparation protein under the conditions of the assay. Cholinesterase is normally low or non-detectable in crotaline venoms. The high activity of the *Natrix* saliva is surprising. Subsequent tests showed that the *Natrix* preparation was 50 per cent inhibited

by 10^{-2} molar hexamethonium (1,6-bis hexane trimethylammonium); completely inhibited by 10^{-4} and 90 per cent inhibited by 10^{-6} molar concentrations of neostigmine (prostigmine), respectively. This preparation did not appear to hydrolyze either benzoyl choline or acetyl β-methyl choline. Characteristically, elapine venom cholinesterase does not act on benzoyl choline, but will hydrolyze acetyl β-methyl choline. It was unfortunately impossible to treat the *Alsophis* preparation to this sort of analysis due to its low activity and a waning supply of preparation.

VIII. Discussion

The statement that a particular animal is or is not "venomous" is outwardly a qualitative judgment, but it conceals a quantitative statement. The demonstrated presence of enzymes characteristic of venom in *Alsophis'* saliva constitutes necessary but not sufficient proof for the postulated function of the secretion in subduing prey.

Alsophis' saliva protein content and the relatively greater activity of that protein are superior to those found in the "nonvenomous" *Natrix*. Two large teeth surrounded by a fleshy ridge in the rear of the upper maxilla appear to be modified for administration of the saliva. Although these rear teeth are not grooved, the total picture for *Alsophis* indicates a degree of specialization trending in the direction of the adaptations of the truly venomous species. However, these morphological features, like the relative potency of the salivary secretion, are only an indication of the possible function. Critical evidence with regard to the use and thus the significance of the "venom" will probably come from the careful study of feeding behavior.

Animals killed by snake venom decompose at a much more rapid rate than similar individuals who have died peacefully (Zeller, 1948). Vipers, kept from injecting venom by fang removal or ligature of the duct, take from two to three times the normal time to digest a food object of constant size. Apparently the digestive function of venom is a large part of its adaptive significance, especially in an animal unable to mechanically masticate its prey. It may be that at the level of development seen in *Alsophis*, the effect of the saliva in subduing prey is secondary and gratuitous to the digestive function. At higher levels of specialization it is almost impossible to disentangle the two roles. The enzymes of snake venom are most easily interpreted as a digestive complex (Zeller, 1948).

The cholinesterase of *Natrix* saliva, unlike the usual elapid type (Zeller, 1947), will not hydrolyze acetyl β-methyl choline. This is especially interesting in light of the problem of the relationships between the colubrids and elapids (Johnson, 1956). An enzyme study of the analogous secretions of these two groups in a larger range of genera could prove valuable. It would, of course, first be necessary to establish the stability of enzyme type as a character within a genus or genera for which the relationships are relatively clear.

Acknowledgments

I would like to acknowledge the guidance and suggestions of Dr. William R. Sistrom, who cheerfully permitted a small plague of snakes in an otherwise orderly bacteriology laboratory. I am also indebted to Mr. A. S. Rand and Dr. E. E. Williams for suggesting the problem, supplying valuable advice and information, and seeing the paper through several revisions. Dr. Karl Kofford generously supplied the *Alsophis portoricensis* used.

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BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. APRIL 7, 1961 No. 135

NOTES ON HISPANIOLAN HERPETOLOGY

2. A REVIEW OF THE *ANOLIS SEMILINEATUS* GROUP WITH THE DESCRIPTION OF *ANOLIS COCHRANAE*, NEW SPECIES

BY ERNEST E. WILLIAMS
and A. STANLEY RAND

INTRODUCTION: Recent investigations in Haiti and the Dominican Republic by expeditions from the Museum of Comparative Zoology have added considerably to our knowledge of the distribution of the so-called grass-anoles of the *semilineatus* group and have resulted in the discovery of a third member of the series in the Cordillera Central of the Dominican Republic. In addition to describing the new species just discovered we here attempt a summary of the information now available on this group.

ACKNOWLEDGMENTS: The new species was collected in the summer of 1958 by Clayton E. Ray and A. Stanley Rand during an expedition partly supported by a grant from the Society of Sigma Xi and enjoying the cooperation of the University of Santo Domingo and of the government of the Dominican Republic. The essential and generous aid of Dr. Eugenio de Jesus Marcano, who accompanied the expedition, and the use of a car and driver furnished by the University of Santo Domingo are very gratefully acknowledged. In August 1959, E. E. Williams and A. S. Rand collected in the vicinity of Port-au-Prince with the support of National Science Foundation Grant NSF G-5634. In 1960 A. S. Rand and J. Lazell collected around Port-au-Prince in northern Haiti and near Aux Cayes on the southwest peninsula, aided by a grant from the American Philosophical Society. In both Haitian trips the letters provided by M. Gerard Philippeaux, Minister of Agriculture, and the willing assistance of M. Leonce Bonnefil fils, zoologist in the Department

of Agriculture and Natural Resources, were indispensable elements in the success of the venture.

In addition to the specimens collected by these expeditions and those already present in the Museum of Comparative Zoology (MCZ), material was obtained on loan from the United States National Museum (USNM) and the American Museum of Natural History (AMNH). The assistance of the curators of these collections is gratefully acknowledged. Dr. P. S. Humphrey made available for study material collected by him for Yale Peabody Museum (Yale) and the University of Florida (UF).

THE PREVIOUSLY KNOWN SPECIES: In order to provide a frame of reference for the new species, we first summarize the knowledge now at hand for the previously known species: Two species of "grass anoles," *A. semilineatus* Cope and *A. olssoni* Schmidt, have long been known in Hispaniola. Both are small (*ca.* 40 mm snout-vent length), slender-bodied forms with elongate heads, a dorsal zone of about 10 rows of enlarged keeled scales as large as the strongly keeled belly scales, tail only slightly compressed and with no clear demarcation of the breaking zones or verticils. They are thus a morphologically strongly marked group within the Hispaniolan anoles. In habits they are also distinctive, being associated characteristically with grass and low bushes.

MORPHOLOGY: (See also table, below). Structurally the two species differ very little — they differ in size of scales and slightly in body size, tail length and shape of head but in none of these regards so strikingly that instant identification can be confidently made even by the experienced worker. Body coloration differs also but not without some puzzling cases. The dewlap in males, both as to color and squamation, is the diagnostic difference easiest to employ. The dewlap skin in *A. semilineatus* is white and the gular scales about the same size as the ventrals. In *olssoni* the dewlap skin is red or orange (darkly pigmented in alcohol) and the gular scales up to three times as large as the ventrals. In life the iris of *semilineatus* is steel blue, that of *olssoni* dark brown. This difference is not determinable in alcoholics.

ECOLOGY: There exists a real ecological difference between the two species but again there is overlap and the species do occur side by side.

Mertens (1939) describes *A. semilineatus* as "eurytop" occurring in both dry and wet areas. He found it in mangroves (Puerto Plata, Sabana de la Mar), corn fields (Moca), dry open brush (Barahona, San Pedro de Macoris, Ciudad Trujillo), meadows

in the lower drier pine woods (Jarabacoa, Moncion), and in damp lush vegetation (Samana, the top of the pass between Santiago and Puerto Plata). He, in fact, states that it is absent only in the cactus- steppe. Rand (1958, field observations) saw it in the Dominican Republic primarily in open situations and along roadsides and in pastures but found also a single specimen sitting on a rock in a muddy trail through heavy forest (Bejucal), and a dense population living in low vegetation in an area of rather dense bamboo along a stream bank (nr. Sabana de la Mar). Hassler (field notes for November 4, 1929) reports finding this species at Laguna near Samana on "leaves in damp woods and in fields nearby."

Near Port-au-Prince, *semilineatus* occurs in the hills to the south of town and up to the vicinity of Furcy at 4000-5000 ft. It is absent from Port-au-Prince itself and from the Cul de Sac Plain. In one place it has been observed to overlap with *olssoni* (see below).

Mertens has described *A. olssoni* in contrast to *A. semilineatus* as "stenotop," confined to open dry areas. It seems, indeed, to be more limited than *semilineatus*, but in 1959 Williams and Rand found it in the moderately dense vegetation of a Port-au-Prince garden and also in the irrigated areas of the experimental farm at Damien, Haiti. It is present in open thorn scrub of the Cul-de-Sac Plain both in Haiti and in the Dominican Republic. It is known to occur with *semilineatus* at several localities. Mertens records both forms from the vicinity of Ciudad Trujillo, and at Moncion, Sabana de la Mar and Barahona, all localities in the Dominican Republic. Cochran reports both species at San Michel du Nord, Haiti. In 1960 Rand and Lazell obtained both species at Gros Morne in northern Haiti. They found "*A. olssoni* on grass and low vegetation along sunny roadsides, *A. semilineatus* on vegetation at the edge of forest."

In August 1959 Williams and Rand studied a contact area between *semilineatus* and *olssoni* on Bontillier Road which climbs the foothills south of Port-au-Prince. *A. olssoni* occurred only on the lower reaches of the road, *A. semilineatus* only on the portion of the road which parallels the crest of the hill. No striking vegetation or habitat difference was evident between the two portions of the road, both of which traverse very disturbed, cut over, areas. The distance between the places at which *semilineatus* and *olssoni* were found closest to one another was a matter of a few vertical yards. Rand and Lazell returning

to the same area in 1960 found the same general pattern but in one instance a *semilineatus* was taken about 20 feet from an *olssoni* and at the same level.

Habits: The two species differ very little in habits. Both are commonly seen on grass stems and the slender twigs of small bushes and plants. Sometimes they occur on fence posts and stands of barbed wire and occasionally on the ground. None have been seen on the trunks or in the crown of even small trees. Numbers of *A. olssoni* were observed by Williams and Rand at Damien, Haiti. Individuals of all sizes were found in the tall grass, while on the fence posts most of the animals were large males, and in the short 4-8 inch grass most were juveniles. They are frequently found facing head downward on a vertical perch with the neck bent so that the head is almost horizontal. Both sleep with the hind legs fully extended. Both escape by jumping off their perch into grass cover nearby. In one area near Port-au-Prince a few individuals were chased out of the grass into a rock pile. Here they did not go deep into the rock pile in contrast to juvenile *A. cybotes* but hid close to the surface and could usually be chased out by poking into the holes with a short stick. *A. semilineatus* is perhaps shier than *A. olssoni* and, according to Mertens, it is less pugnacious. Mertens reports that freshly caught *olssoni* carried out biting battles with each other, raising the nuchal crest and displaying their dewlaps.

Very little is known of the reproductive habits of these forms. There is one observation by Rand (field notes, 1958) on *A. semilineatus* in the Dominican Republic: "In one locality (Rancho La Guardia, San Rafael Province) in a coffee plantation about twenty yards from open pasture, a number of eggs of this species were found. These were discovered in three of 22 rotten logs examined in a small area. One log contained 12 eggs, another 7 eggs, and the third 4 eggs. These three logs differed from the others examined in that they contained nests of a large black stinging ant. The eggs were mostly in the loose soil just under the logs but some were in the galleries of the ant nest. When I picked up the first egg an ant stung me and my involuntary jump sent the egg flying several feet. The other logs in the area contained a variety of invertebrate life but the ones with the lizard eggs had only the black ants and a single centipede nest. The ants provided an effective protection for the lizard eggs and it seems possible that the lizards had sought out these nests in which to lay their eggs.

The eggs were ovoid with a white flexible skin. They ranged in size from 12 by 9 mm to 7 by 6 mm. Collected on August 13 fourteen of the twenty-two eggs hatched, the first on August 15 and the last on September 17."

DISTRIBUTION: Both species are very widely dispersed in Hispaniola. Because of their ecological differences the two distributions coincide only in limited and scattered areas, though in broad terms they overlap widely. No *olssoni* are at present known from the Samana peninsula and the adjacent areas in the north of the Dominican Republic north of La Vega and east of Puerto Plata, or from ths southwestern peninsula of Haiti, but none of these areas is so well collected that the absence of *olssoni* from collections can be taken as a demonstration of a real absence in the field. Except perhaps in the southwestern peninsula, the distribution can be interpreted better in terms of present ecology than in terms of any other factor. We list all the verified localities[1] for the two species below:

SEMILINEATUS. **HAITI:** *Dept. du Nord*, Cap Haitien (MCZ, USNM), Citadelle (MCZ), Dondon (MCZ); *Dept. de l'Artibonite*, Gros Morne (MCZ), San Michel (USNM); *Dept. de Ouest*, Basin Bleu nr Furcy (MCZ), Bontillier Road nr Port-au-Prince (MCZ), 5 km south of Dufort, south of Leogane (MCZ), Furcy (MCZ, AMNH), Obleon nr Furcy (MCZ); *Department du Sud*, Miragoane (MCZ), Les Platons north of Aux Cayes (MCZ), Place Negre near Jeremie (MCZ). **DOMINICAN REPUBLIC:** *Prov. San Rafael*, Rancho La Guardia (MCZ); *Prov. Barahona*, Barahona (AMNH, Senckenberg), Palo (AMNH); *Prov. Benefactor*, 7 km north of Carpintero (MCZ); *Prov. Santiago Rodriguez*, Moncion (Senckenberg); *Prov. Santiago*, top of pass between Santiago and Puerto Plata (Senckenberg); *Prov. Puerto Plata*, 8 km north of Peña (MCZ), Balneario Colon, Puerto Plata (Senckenberg), Rio Munoz, 7 km from Puerto Plata (Senckenberg); *Prov. La Vega*, Jarabacoa (Senckenberg); *Prov. Espaillat*, Moca (Senckenberg), Rio San Juan (USNM); *Prov. Duarte*, Las Bracitas (AMNH); *Prov. Trujillo*, nr San Cristobal (MCZ); *Prov. San Pedro de Macoris*, San Pedro de Macoris (Senckenberg); *Prov.* Seibo, Boca del Inferno (USNM); San Francisco, 6 km east of Hato Mayor (MCZ); Rio Yabon

[1] The record of *semilineatus* for the island of Navassa is doubtful. A paratype of *A. olssoni* was recorded by Schmidt (1919) as probably from this island. In 1921 Schmidt redetermined the specimen as *A. semilineatus* and cited the species without qualification as a member of the Navassa fauna. No additional specimens of *A. semilineatus* have been collected, and the record is unconfirmed.

(MCZ); *Prov. Samana,* Laguna (AMNH), Samana (MCZ, Senckenberg), Sanchez (MCZ); *Distrito de Santo Domingo,* Ciudad Trujillo (Senckenberg).

Olssoni. **HAITI:** *Dept. du Nord Ouest,* Bombardopolis (MCZ), Jean Rabel (MCZ, AMNH), Môle St. Nicolas (MCZ); *Dept. du Nord,* Cap Haitien (USNM); *Dept. de l'Artibonite,* bridge over the Artibonite (MCZ), south end of Etang Bois Neuf (MCZ), Gros Morne (MCZ), St. Marc (USNM, AMNH); *Department de Ouest,* Boutillier Road nr Port-au-Prince (MCZ), Carrefour (AMNH, Yale, UF), Cabrite Id (AMNH), Damien (MCZ), Delmas (MCZ), Diquini (MCZ, USNM), Eau Gaillee (Yale, UF), Etang Saumatre (MCZ), Fond Parisien (AMNH), Hatte Latham (MCZ, USNM), Manneville (MCZ), Mon Repos (USNM), Morne Decayette (MCZ), Petionville (Yale, UF), Port-au-Prince (MCZ, USNM, AMNH, Yale, UF), Ste. Philomene (USNM), Thomazeau (MCZ), between Thomazeau and Manneville (MCZ), Trou Caiman (USNM), Trou Forban (MCZ), *Gonave Id,* Anse a Galets (MCZ), Encafe (MCZ, USNM, Yale), Pointe-a-Raquettes (Yale, UF). **DOMINICAN REPUBLIC:** *Prov. Monte Cristi,* Monte Cristi (AMNH, Senckenberg); *Prov. San Rafael,* Banica (MCZ); *Prov. Independencia,* Las Baitoas (AMNH), Duverge (AMNH); *Prov. Barahona,* Barahona (AMNH), Senckenberg), Cabral (MCZ); *Prov. Santiago Rodriguez,* Moncion (Senckenberg); *Prov. El Seibo,* Sabana de la Mar (Senckenberg); *Distrito de Santo Domingo*: Ciudad Trujillo (Senckenberg).

A third species discovered: On September 7 to 8, 1958, collecting in the vicinity of Constanza in the high interior of the Dominican Republic, C. E. Ray and A. S. Rand of Harvard University and Sr. Eugenio de Jesus Marcano of the Universidad de Santo Domingo obtained 20 specimens of a new species of "grass anole." The greater number of these specimens were collected at night, sleeping on grass stems. A renewed effort to collect the same form the next morning obtained very few individuals, the lizards being then very wary and difficult to see or catch.

Examination of these specimens reveals that they differ from the two previously known species in just the ways cited by Doris Cochran (1941, pp. 139-140) for a single specimen from Constanza which she then referred hesitantly to *A. olssoni.* Her remarks are quoted in full:

"With some doubt I place with *Anolis olssoni* a single adult male (USNM No. 62103) collected by Dr. W. L. Abbott in the hills 5 miles south of Constanza. This individual has much smaller scales on the gular fan than does typical *olssoni* from San Michel, Haiti. It does not approach, however, *semilineatus* in fineness of scales. In fact, while the gular scales are finer, the dorsal and ventral scales of the Constanza lizard are actually perceptibly coarser than they are in the San Michel specimens. The color pattern of this Constanza specimen shows none of the definite black markings that so often appear on true *olssoni*. It is lilac gray above, tinged with china-blue on the supraocular region, the dorsal tone shades into drab above the lateral light stripe, which is very sharply marked anteriorly but less so after it passes the shoulder, back of which it fades out almost completely. The only definite head marking is a black diagonal bar across the temporal region which does not occur in *olssoni* but is found in every specimen of *semilineatus*. A series of examples from Constanza will be needed to determine whether these characters are stable and definite, meriting specific separation or whether they represent an aberrant or hybridized *olssoni* with some of the *semilineatus* characters."

Dr. Cochran has excellently characterized the new species, which may therefore be appropriately named:

ANOLIS COCHRANAE new species

Type. MCZ 57660, an adult ♂ collected at Constanza, Dominican Republic, September 7-8, 1958 by C. E. Ray, A. S. Rand, E. de Jesus Marcano.

Paratypes. MCZ 57661-79, same data as above: USNM 62103, hills 5 miles south of Constanza, collected by Dr. W. L. Abbott, April 29, 1919.

Diagnosis. An *Anolis* allied to *semilineatus* and *olssoni*, differing from the first in the much larger dorsal, ventral and supratemporal scales, from the latter in having a white rather than a red or orange dewlap in the somewhat larger dorsals and in having the gular scales little if at all larger than the ventrals, differing from both in having the ventrals nearly as large as the enlarged dorsals.

Description. Head: All head scales multicarinate rather than smooth or singly keeled. Five to eight scales across head between second and third canthals (usually six to seven). Frontal depression very shallow, the scales in it nearly or as large as the posterior frontal or anterior supraorbital.

Supraorbital semicircles in contact (five specimens) or separated by one scale row (fifteen specimens), wholly or partly separated by one scale row from the supraocular discs. Supraocular disc consisting of two to five large keeled scales separated from the elongate supraciliaries by at least two rows of scales. Canthus distinct, canthal scales four (five in one specimen), the second largest diminishing gradually forward. Naris anterior to canthal row. The anterior nasal scale in contact with rostral. Loreal rows four to five (three on both sides in one specimen). Temporal scales subgranular. Supratemporal scales larger, keeled, grading into the large keeled scales surrounding the interparietal. Interparietal larger than ear, separated from the supraorbital semicircles by one to three scales (usually two).

Posterior frontal as large as anterior supraorbital. One scale nearly as large as the posterior frontal between the latter and the canthals.

Suboculars in contact with supralabials. One scale intervening between subocular series and canthals. Five to six (six on one side, seven on the other in one specimen) supralabials to the center of the eye.

Mentals wider than long, one to two scales inserted between the tips posteriorly. One sublabial on each side in contact with the infralabials. Central throat scales keeled, elongate. Gular fan in males.

Trunk: About ten longitudinal rows of much enlarged keeled middorsal scales, broader than long, as large as the ventrals (10 to 12 in standard distance), grading laterally into the smaller flank scales which in some specimens are keeled imbricate, in others nearly granular. Ventrals in longitudinal rows, keeled, imbricate, mucronate. Postanal plates present in males. Scales of gular fan moderate, not extremely elongate, hardly larger than ventrals, not clearly arranged in lines.

Limbs and digits: Hand and foot scales multicarinate, about 17-19 lamellae under phalanges 2 and 3 of fourth toe, about 26-31 under whole toe. Largest arm and leg scales unicarinate, about as large as ventrals.

Tail: Tail subcircular in section, very long, more than 2½ times snout-vent length; verticils not apparent.

Size: Largest ♂ 41 mm in snout-vent length; largest ♀ 38 mm snout-vent length.

Color: Essentially as in *semilineatus*.

The more significant characters of *cochranae* may be compared with those of *semilineatus* and *olssoni* in tabular form:

semilineatus	*olssoni*	*cochranae*
skin of gular fan white	skin of gular fan orange to red	skin of gular fan white
flank stripe short	flank stripe long	flank stripe short
gular scales ca. = ventrals	gular scales>> ventrals	gular scales ca. = ventrals
14-17 enlarged dorsal scales in distance snout to middle of eye (standard distance)	11-13 enlarged dorsal scales in standard distance	10-12 enlarged dorsal scales in standard distance
median rows of enlarged dorsal scales about as broad as long	median rows of enlarged dorsal scales mostly longer than broad	median rows of enlarged dorsal scales about as broad as long
17-21 ventrals in standard distance	11-14 ventrals in standard distance	11-14 ventrals in standard distance

Other differences have been listed by Mertens or Cochran, but they are at best modal differences or they alter markedly with age. These species are indeed close, and females and juveniles are sometimes difficult to distinguish.

Discussion: *Anolis cochranae* combines in new ways characters of *A. semilineatus* and *A. olssoni*. It is in no sense an intermediate; its characters are either those of one or the other or are somewhat exaggerated versions of a trend present in one.

It is necessary to admit that we know very little about this species beyond its existence. Its distribution would appear, on present evidence, to be extraordinarily limited. It may well be confined to the high interior, but its real range is surely more extensive than known at present. The area from which it comes is remarkable for certain peculiar forms: *Celestus darlingtoni* and *Audantia shrevei* in the higher elevations, *Anolis aliniger* (described as a subspecies of *A. chlorocyanus* by Mertens in 1939 but in reality a full species) in the vicinity of Constanza itself, *Anolis darlingtoni* both from Constanza and from higher elevations. The region merits extensive and systematic collecting.

The biological relation of *A. cochranae* to the other two members of the *semilineatus* group is equally unknown. We do not

know its contacts with either form. Its relationship to *A. semilineatus* in particular is puzzling. In squamation it differs strongly enough that we have called it, as a matter of judgment, a distinct species. The scale differences from both *semilineatus* and *olssoni* are as great or greater than the differences between other closely related sympatric fully valid species. But in other *Anolis* such (or lesser) differences are correlated with color and dewlap differences that are evident visual cues to species recognition. In color and dewlap *A. cochranae* exactly resembles one of the neighboring species — *semilineatus*. If *A. cochranae* is indeed a full species that is at some point in contact with *semilineatus*, it is necessary to suppose that there is some unknown behavioral difference that maintains the distinctness of the population in the absence of color cues.

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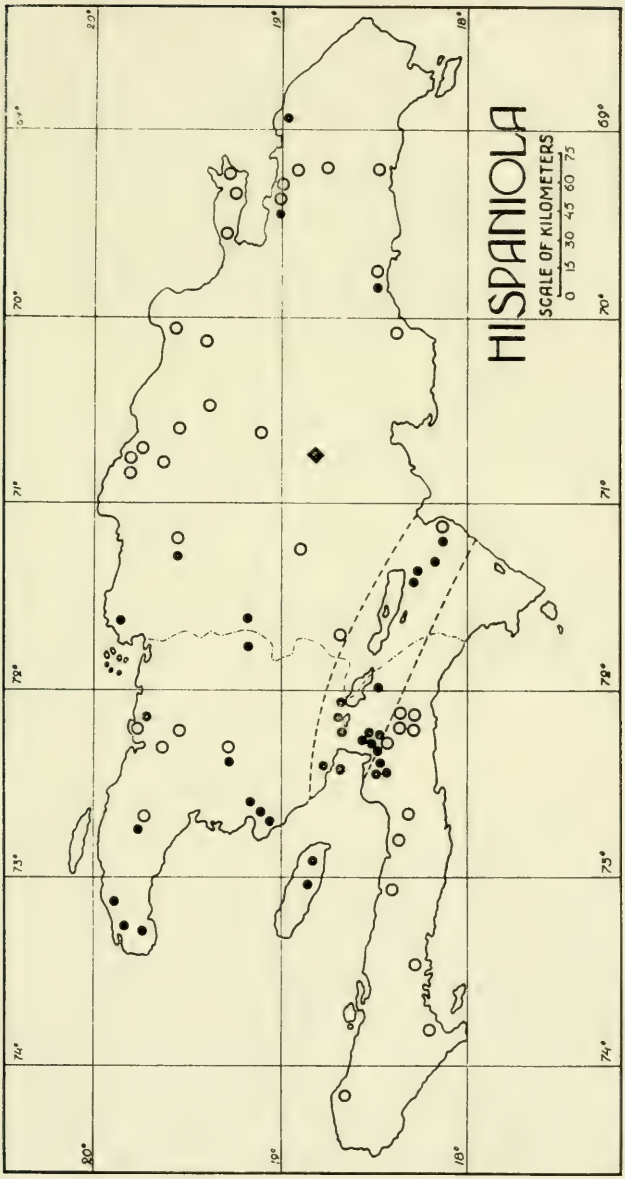

Map: Distribution of the three species of the *Anolis semilineatus* group in Hispaniola.

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NOTES ON HISPANIOLAN HERPETOLOGY 3. THE EVOLUTION AND RELATIONSHIPS OF THE *ANOLIS SEMILINEATUS* GROUP

BY ERNEST E. WILLIAMS

The discovery of a third species of the *Anolis semilineatus* group, confined apparently to the high interior of the Dominican Republic, poses problems in the distribution, biology and evolution of the group.

The distributional data for the *semilineatus* group has been given in Williams and Rand (1961) and need not be repeated in detail here. *A. semilineatus* and *A. olssoni* are both widely distributed north of the Cul de Sac Plain but occupying ecologically somewhat different situations and thus with but limited actual contact or overlap; only *A. semilineatus* at present is known south of the Cul de Sac Plain in the southwest and Barahona peninsulas.

A. cochranae is found in the center of Hispaniola in the Cordillera Central — geographically in the midst of the other two species though its contacts with these others are not known. The biological peculiarity in the relation of *A. cochranae* to *A. semilineatus* has also been pointed out in Williams and Rand (1961). Thus, though differing strongly from the closely related *A. semilineatus* in certain scale characters, *A. cochranae* is identical in body and dewlap color. This phenomenon is highly unusual in the genus *Anolis* in which body and dewlap color differences are important cues in species recognition. (There are, for example, strong body and dewlap color differences between *A. semilineatus* and *A. olssoni*.) *A. cochranae*, if it is in contact with *A. semilineatus*, as *A. semilineatus* and *A. olssoni* are in contact with one another, would seem to be a most anomalous case in which it would be necessary to provide some *ad hoc* explanation — such as some unknown behavior difference — for the maintenance of the species distinction.

The problem is thus to provide an explanation of the central geographic position of *Anolis cochranae* in Hispaniola and of the curious absence in *cochranae* of the usual anoline species recognition characters *contra* a related species that occurs literally on every side of it.

I propose below a suggested history of the *semilineatus* group that appears to solve this problem. It must be admitted that this proposed history depends upon taking at face value the distributions of the three species as they are known at present. This is patently unsafe, but it provides a useful starting point.

On our present knowledge of distribution it is simplest to suppose that the postulated biological problem has not arisen, that *cochranae* and *semilineatus* are nowhere in contact. This is at the moment only a brave hypothesis. *Anolis cochranae* is known from only two collections; our more extensive knowledge of the distributions of *semilineatus* and *olssoni* is by no means good enough to prove contact or absence of contact with *cochranae*.

Critical to the proposed history is the supposition — uncontradicted by the available evidence — that *olssoni* is really absent from the southwest and Barahona peninsulas. It does appear to be absent from the moist coastal zone at Aux Cayes (observations by A. S. Rand and J. Lazell in 1960) and Rand did not collect it in the dry area of Oviedo on the Barahona peninsula in 1959. It is not present in Hassler's collections from these two areas.

Let us then take the present distributional evidence at face value. Let us assume then that *semilineatus* is the only grass anole of the southwest and Barahona peninsulas and that *olssoni* just touches this area at the southern edge of the Cul de Sac Plain.

The southwest and Barahona peninsulas taken together are just that portion of the island which was cut off from the mass of Hispaniola by the Pleistocene seaway through what is now the Cul de Sac Plain. Residual salt lakes and coral rocks still testify to this former seaway.

The division of Hispaniola into two parts which resulted from this seaway provides two suitable theatres — a main island and a southern counterpart — for the classic pattern of speciation during separation, and intensification of species difference ("character displacement") during renewed contact.

On this hypothesis *semilineatus* is the autochthonous grass anole of the southern cut-off portion of Hispaniola and *olssoni*

and *cochranae* autochthons of the northern main mass of the island. *Semilineatus* has infiltrated the northern island all but completely, while *olssoni* is not known to have invaded the southern island.

The spread of *semilineatus* through much of the northern island is not too surprising in view of its eurytopic ecology (Mertens, 1939, Williams and Rand, 1961). Though characteristic of a specialized open habitat, it seems to be sufficiently tolerant of forests that these would be less efficient barriers to its spread than they would to stenotopic *olssoni*. It is somewhat more surprising — if it is true — that *olssoni* has not spread along the dry north coast of the southwest peninsula or the east coast of the Barahona peninsula, but it would be stopped easily by discontinuities in suitable habitat and would for this reason be unlikely to reach localities otherwise quite suitable to it on the southern island.

The different coloration in *olssoni*, including the dewlap color, and the large size of the dewlap scales may well have developed after *olssoni* came into secondary contact with *semilineatus* during the latter's invasion of the northern island fragment. In suggesting this we assume that the features in common of *cochranae* and *semilineatus* are primitive and that modification in these features took place exclusively or almost so in *olssoni*. (Surely the lack of enlargement in the gular scales is primitive in *semilineatus* and *cochranae;* this leaves only color in question.)

What, however, about the origin and relationship of *cochranae* and *olssoni?* It must first be noticed that there is some plausibility in considering these two more closely related to each other than to *semilineatus*. In body squamation (i.e. scale size), *cochranae* and *olssoni* are very similar. This is a feature which, unlike the characters of the dewlap or of body pattern, is unlikely to be a matter of intra- or inter-species recognition. We do not know that it is *per se* adaptive: the difference in scale size between *semilineatus*, on the one side, and *cochranae-olssoni*, on the other, is more likely to be the external expression of more fundamental genetic divergencies.

No physiographic barrier, however, will account for the division of the grass anole population of the northern or main Hispaniolan island into two species. It is necessary to suppose that the barrier was an area of unsuitable ecology, i.e. moist dense forest. *Olssoni* may then be supposed to have arisen in

the arid coastal lowlands while *cochranae* arose in the open areas of the high pine woods[1] of the interior valleys of the Cordillera Central. (We note that Wetmore and Swales, 1931, p. 24, describe the natural vegetation of the Valle Constanza as "forests of open pine mingled with areas of dense rain forest.")

The known habitat of *cochranae* — Valle Constanza — is a high interior valley of the Cordillera Central. Though the floor of this valley is not very high (*ca.* 3000 feet) it is surrounded by some of the highest peaks in Hispaniola and ingress to it at moderate elevations is somewhat narrow and limited. In such an area a grass anole population might indeed enjoy a measure of isolation from other grass-bush populations — the more so if we suppose that the separation of *olssoni* and *cochranae* dates from a period in which the density of the hardwood forest of intermediate elevations was at a maximum.

Relationships of the *semilineatus* group.

There are no other anoles in Hispaniola which either very much resemble or seem very closely related to the *semilineatus* group. A search for close relatives and ancestors takes us at once outside Hispaniola.

Two Greater Antillean groups of *Anolis* are structurally similar — the *alutaceus-clivicolus-cyanopleurus-spectrum* group in Cuba and the *krugi-pulchellus-poncensis* series in Puerto Rico. (None of the anoles of Jamaica or the Bahamas are similar either ecologically or structurally.)

Both the Cuban and the Puerto Rican series share with the *semilineatus* group the middorsal zone of enlarged scales (least developed in *krugi* of Puerto Rico). All except *alutaceus-clivicolus* have keeled ventrals.

The Cuban anoles are all forest species, *A. alutaceus* occurring in rather deep shade, *A. spectrum* in less deep shade. But, though in this regard they differ from the Hispaniolan species which are fonder of open areas, they are closer to the *semilineatus* group in structure than are the Puerto Rican species. Like the *semilineatus* group they are small, usually under 40 mm snout-vent length, slender, with large dewlaps and well developed postanal scales in the males. In color, however, they differ in never possessing the flank stripe so characteristic of the *semilineatus* group, tending instead to emphasize the light middorsal stripe.

[1] Pine in Hispaniola, in contrast to e.g. Cuba, is confined to higher elevations.

Of the *alutaceus* series, *clivicolus*, which may be a subspecies of *alutaceus*, has the least slender habitus and the least specialized squamation. It is easy to envision this as representing the primitive stock of this series.

The Puerto Rican series is, on the other hand, more similar to the Hispaniolan species in habits. Two of the three species — *pulchellus* and *poncensis* — are "grass anoles" or at least anoles of open reaches. The third species — *krugi* — is an anole of denser brush. All are larger than any species of the *semilineatus* group — nearer 50 mm than 40 mm snout-vent length. They are perhaps not as slender as their parallels in Hispaniola (though this is a character difficult to estimate objectively); the dewlaps are relatively small and the postanal scales poorly developed. All three have a flank stripe passing forward through the eye more or less well expressed.

In both Cuba and Puerto Rico the series exhibit a wider range of structure than do the Hispaniolan forms. In each series there is a species with the middorsal zone of enlarged *keeled* scales less developed than in any Hispaniolan species (in Cuba — *clivicolus-alutaceus*, in Puerto Rico — *krugi*) and one with this zone much more strongly developed than in any Hispaniolan species (in Cuba — *spectrum*, in Puerto Rico — *poncensis*). One difference appears in this regard: in all the Cuban forms the width of the zone of enlarged dorsal scales is about the same (*ca.* 8 scale rows as compared with *ca.* 10 in Hispaniolan forms), while in the Puerto Rican forms concurrently with increase in the size of the middorsal scale zone, there is an increase in the number of rows enlarged (*ca.* 4 in *krugi*, *ca.* 12 in *pulchellus*, 15+ in *poncensis*).

The evaluation of these resemblances, which are in each case beset with significant differences, is difficult. Parallelism is very probable, and it is especially likely that the Puerto Rican series is an independent radiation within Puerto Rico from the same stock that gave rise to *A. cristatellus*, *A. stratulus*, *A. gundlachi* and *A. evermanni*. The primitive member of the Puerto Rican series, *A. krugi*, is not very different from *cristatellus* and *gundlachi* and would certainly be classed with them except for its obvious position at the base of a small grass anole radiation on Puerto Rico.

The Cuban anoles which display a strong structural affinity *in spite of some habitat difference* are more probably close relatives of the Hispaniolan series. There is in fact no substantial reason for doubting the relationship.

It must be pointed out that the squamation pattern with a strongly developed middorsal zone of enlarged keeled scales, smaller laterals, and strongly keeled ventrals as large or larger than the middorsals is common in mainland *Anolis,* particularly so in Central America. This pattern occurs also in the Greater Antilles in three species which, though certainly anoline, are currently referred to other genera: the Cuban species (*ophiolepis*) to *Norops,* and a species from Navassa (*barbouri*) along with one from Hispaniola (*wetmorei*) to *Chamaelinorops.*

The mainland forms exhibit a whole spectrum of conditions in regard to the distinctness, number of scale rows, size of scales involved in the dorsal zone, etc. No described form seems close enough to the Hispaniolan or Cuban grass anoles to be worth serious consideration as representing the ancestral stock.

Norops ophiolepis, which occupies the grass anole habitat in Cuba, does not seem related either. It has some features peculiar to itself — the reduction of the canthal ridge scales to two, the small number of scales in the loreal area (*ca.* 10-12), the very elongate scales between the nostrils, the large mental scales — that are unlike not only the *semilineatus-alutaceus* groups but its supposed congeners on the mainland. The relationships of *ophiolepis* are probably with *Anolis sagrei* and more remotely with the *homolechis* complex; there are certainly no grounds for postulating close affinity to the *semilineatus-alutaceus* set.

Chamaelinorops barbouri and *C. wetmorei* are even more distinct. The basic pattern of squamation is quite heterogeneous and yet upon this has been imposed a second pattern of enormously enlarged keeled dorsals and hugely enlarged keeled ventrals exaggerated beyond that seen in any other forms.

This picture, like the apparent radiation of forms on Puerto Rico and the extraordinarily varied array of forms on the mainland, suggests strongly that the pattern — enlarged middorsal zone, enlarged keeled ventrals — is one of several stereotypes that the anoles have again and again produced, that this is one of a limited set of squamation patterns possible to the anolines and therefore produced in parallel fashion in many times and places.

It is this parallelism that contributes to the notorious "difficulty" of the genus *Anolis.* Narrow groups are rather easy to recognize (though the specific and infraspecific structure within

the group may be puzzling in the extreme) but wider relationships (at least when externals only are considered) are problematical, becoming obscurer with each step more distant from the species group.

Origin of the *semilineatus* group

The species of the *semilineatus* group are more uniform than the related Cuban series. They most resemble *cyanopleurus,* the middle term in the morphological series of Cuban forms. This species has its range in extreme eastern Oriente and is thus geographically closest to the Hispaniolan group. It therefore seems probable that the *semilineatus* series on Hispaniola has been rather recently derived from a *cyanopleurus*-like Cuban ancestor but has been on Hispaniola long enough to achieve island-wide dispersal and moderate differentiation at the specific level.

Acknowledgments

I have had the advantage of discussions with A. Stanley Rand and with Dr. Richard Etheridge. The latter's osteological evidence for species groupings within *Anolis* (unpublished thesis, University of Michigan) has in part confirmed, in part guided my own thinking on the wider relationships of *Anolis* species.

The map-diagram was prepared by Patricia Grubbs.

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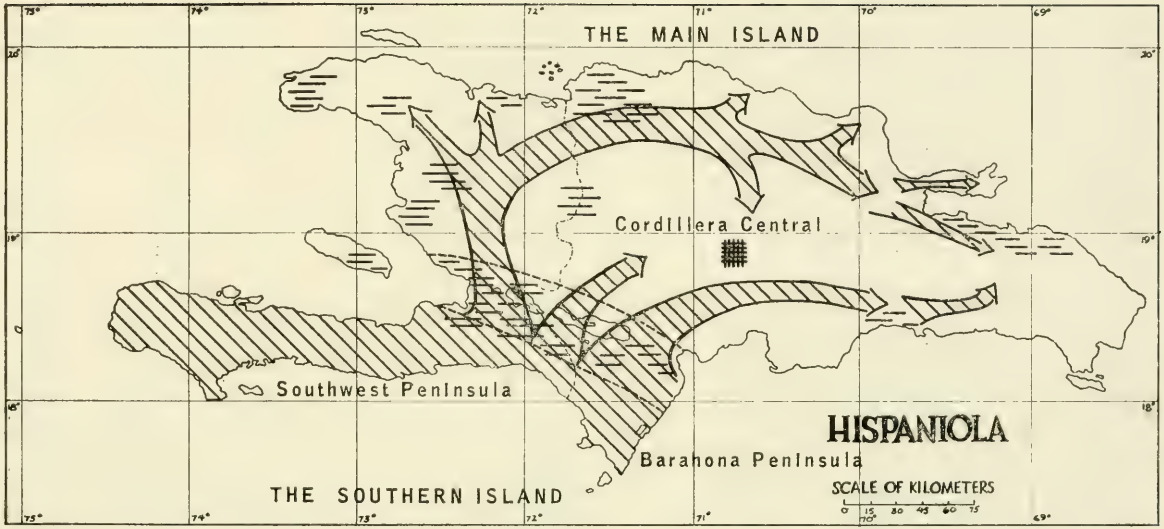

Diagram of the hypothetical invasion of the main mass of Hispaniola by *Anolis semilineatus*. The distribution of *A. semilineatus* is represented as continuous only for sake of convenience. The distributions of *A. olssoni* and *A. cochranae* are, in contrast, represented as disjunct or isolated, to correspond with present information; they may be more extensive or more nearly continuous than is indicated. See map in Williams and Rand (1961) for actual locality records for all three species.

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. APRIL 10, 1961 NUMBER 137

NOTES ON HISPANIOLAN HERPETOLOGY

4. *ANOLIS KOOPMANI*, NEW SPECIES, FROM THE SOUTHWESTERN PENINSULA OF HAITI

BY A. STANLEY RAND

Biological Laboratories, Harvard University

Among the reptiles and amphibians collected for the Museum of Comparative Zoology in Haiti, with the support of an American Philosophical Society grant, during the summer of 1960, are seven specimens that appear to represent an undescribed species of *Anolis*.

These lizards are small, moderately proportioned, dull colored in life, as well in preservative, and rather nondescript animals. In life the adult males possess a dark gray gular fan and an orange-pink chin and throat that distinguish them immediately from any other Hispaniolan *Anolis*. When this chin and throat color disappears in alcohol, the combination of scale characters distinguishes the species, but there are no unique characteristics.

Dr. Karl Koopman, Assistant Curator of Mammals, Chicago Natural History Museum, provided financial assistance and encouragement that helped to make the collection of these specimens possible. In recognition of his aid the new species is called:

ANOLIS KOOPMANI new species

Type. MCZ 62541, adult male.

Type locality. Carrefour Canon, 350 m. altitude, near Ducis, N. of Aux Cayes, Haiti.

Collector. A. S. Rand and J. Lazell, 4 August 1960.

Paratypes. Adult males, MCZ 62542-3; adult females, MCZ 62544-5; young males, MCZ 62546-7. All from Les Platons, 750

m. altitude, above Carrefour Canon, Haiti, A. S. Rand and J. Lazell, 5 August 1960.

Diagnosis. The presence of a zone of much enlarged middorsal scales, keeled head scales, and keeled, imbricate, and pointed ventrals distinguish this species from all the Hispaniolan *Anolis* except those of the *semilineatus* group (*semilineatus, olssoni,* and *cochranae*). It is distinguished from the latter in having 6-8 (not 10) enlarged middorsal rows, 5-8 (not 3-5) loreal rows, and 3-5 (not 1-3) scales separating the interparietal from the supraorbital semicircles. It differs also in coloration, the males having pinkish-orange chin and throat.

Description. (In the following description variations occurring in the paratypes follow, in parentheses, the condition in the type.)

Head. Head scales strongly keeled. Frontal depression moderate. Scales across snout between second and third canthals 8 (7-9). Nares anterior to canthal ridge; separated from rostral by 1 scale. Canthal ridge distinct, not exaggerated, composed of 4 (4-5) large scales preceded by 2 (1-3) small ones. Second canthal largest, third next in size, first and fourth subequal.

Posterior frontal subequal to (slightly smaller than) anterior supraorbital; separated from canthals by 2 (1-2) scales. Anterior supraorbital separated from canthals by 3 (2-3) scales. Supraorbital semicircles separated by 3 (1-3) scales; separated from supraocular disc by one row of small scales (occasional narrow contact). Supraocular disc of 5-6 (5-7) enlarged keeled scales; separated from superciliary by 5-6 rows of granules. A single elongate superciliary. Interparietal scale slightly smaller than ear (½ to slightly smaller); separated from supraorbital semicircles by 4-5 (3-5) scales.

Scales in center of supratemporal area, granular, smaller than flank scales, smallest in center. Scales over temporal bar not (very slightly) enlarged. Temporal scales like supratemporal scales. Suboculars broadly in contact with supralabials, separated from canthals (very narrow contact), not continued behind eye as a series of large scales. Supralabials to center of eye 5 (5-6). Loreal rows 5 (5-8). Loreal scales subequal in size.

Mentals broader than long, in contact with 6 (5-6) throat scales posteriorly. No series of enlarged sublabials. Central throat scales small, elongate, keeled.

Gular fan: Gular fan small. Scales slightly smaller than (subequal to) ventrals, keeled.

Trunk: Middorsal scales much larger than flank scales, grad-

ing into them. Rows of enlarged middorsals 6-8. Ventral scales larger than middorsals, imbricate, keeled.

Limbs and digits: Scales on arms and legs larger than ventrals, multicarinate. Hand and foot scales multicarinate dorsally. Lamellae under phalanges 2 and 3 of fourth toe 18 (17-19). Interdigital pads narrow.

Tail: Tail round in cross-section. Verticils indistinct. Enlarged postanal scales present in males.

MEASUREMENTS

Sex	*MCZ #*	*Snout-vent length*	*Total length*	*Head length*	*Tibia length*	*Hind leg length*
male	62541	34 mm	114 mm	9 mm	11 mm	28 mm (type)
"	62542	39	135	10	12	33
"	62543	38	——	10	12	31
"	62546	23	68	6	7	18
"	62547	21	——	6	7	17
female	62544	33	——	7	9	26
"	62545	33	109	8	10	26

In life a low nuchal and dorsal crest seems permanently raised (absent in females and young males).

Color in life: Male, MCZ 62542, uniform gray-brown above; a whitish line, black edged above, from over shoulder to hind leg, indistinct for the posterior half of its length, below this line the flanks with scattered dark spotting. Belly light brown, chin and throat pale pinkish-orange, with a few scattered black spots, gular fan scales colored like the chin, but the skin dark gray; iris blue.

Female, MCZ 62544, plain brown above, a middorsal stripe with a scalloped margin outlined with darker brown, a yellow stripe from below eye to over shoulder, continued faintly to hind leg; venter yellowish with faint dark spotting on throat; iris blue.

Habitat: The type was taken in a bush along a trail at the edge of a coffee grove. It was found at dusk among small twigs about three feet above the ground where it probably had climbed to spend the night.

Of the six paratypes, three adults were found in heavily shaded coffee groves. All were on the ground among damp leaf litter. One juvenile was found six inches up in low herbaceous vegetation at the edge of the coffee grove. The others were purchased from a small boy for two cents each.

Relationships: The relationships of this species are obscure;

it does not seem to be particularly close to any species now known either from Hispaniola or elsewhere.

The only *Anolis* outside of Hispaniola that are at all similar to this species are the *alutaceus, clivicolus, spectrum, cyanopleurus* groups of Cuba, and this similarity lies primarily in the presence of a zone of enlarged middorsals and does not extend to other details. I interpret this as parallelism.

Within Hispaniola, *A. koopmani* is superficially most like *semilineatus* and *olssoni*. A zone of enlarged middorsals, keeled imbricate, pointed ventrals, keeled head scales, a lateral stripe, narrow digital expansions and small size occur also in *semilineatus* and *olssoni* and suggest a relationship to them. However, most of these characters are not unique to *semilineatus* and *olssoni* even in Hispaniola. The nature of the zone of enlarged middorsals (fewer rows that decrease in size laterally), the strong sexual dimorphism in color, the less attenuate body shape, and generally smaller scales all argue against this relationship.

Anolis ricordi, distichus, cybotes, armouri, shrevei, chlorocyanus, coelestinus and *Chamaelinorops wetmorei* all have specializations that seem to exclude them from close relationships with *koopmani*.

The remaining species, *Anolis monticola, darlingtoni, christophei, hendersoni, baharucoensis* and *Xiphocercus darlingtoni* are poorly known. It is possible that some if not all of them are closely related to one another and that *koopmani's* relationships lie with these. However, until more information is available for this assemblage of species, particularly in regard to color in life, behavior and ecology, this hypothesis must remain very tentative.

Acknowledgments: I am grateful to Dr. Ernest E. Williams for his advice and to Mr. James Lazell and M. Luc Whiteman for their assistance in the field. I wish also to thank M. Leonce Bonnfil fils and the other members of the Department of Agriculture of Haiti who helped us in so many ways.

B R E V I O R A

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PFEIFFER'S UNFIGURED SPECIES OF *STROPHOCHEILUS (MEGALOBULIMUS)*

By T. E. Crowley and T. Pain

This paper is a supplement to J. C. Bequaert's "Monograph of the Strophocheilidae, a Neotropical Family of Terrestrial Mollusks" (Bull. Mus. Comp. Zool., Harvard, **100**: 1-210, 1948).

When Dr. J. C. Bequaert published his monograph on the Strophocheilidae he was unable to deal in detail with two species described by Pfeiffer from specimens in the Cuming collection, now in the British Museum (Natural History), London. Neither of these had ever been figured, and the types are so far the only specimens known. Opportunity has, therefore, been taken to complete Dr. Bequaert's monumental work with figures of Pfeiffer's almost unknown species. In addition we are describing and figuring *S. (M.) capillaceus* (Pfeiffer), so far unfigured, and *S. indigens* Fulton.

The authors wish to express their grateful thanks to the British Museum authorities for permission to examine and photograph the types for reproduction herein, to Dr. R. Zischka for specimens of *S. (M.) indigens* Fulton, to Drs. W. Blume and W. Weyrauch for the loan of material, and to Mr. S. P. Dance and Mr. J. A. Willson for their generous assistance in photographing specimens.

Strophocheilus (Megalobulimus) hector (Pfeiffer)

Plate 1, Figure 1

Bulimus hector Pfeiffer 1857, Malak. Blätt., **4**, p. 157 (Brazil); 1859, Monogr. Helic. Viv., **4**, p. 367; 1868, *Op. cit.*, **6**, p. 11; 1876. *Op. cit.*, **8**, p. 15; 1877, *Op. cit.*, **8**, p. 604. Paetel, 1889, Cat. Conch. Samml., 4th ed., **2**, p. 212.

Bulimus (Borus) hector von Martens 1860, in Albers, Die Heliceen, 2nd

ed., p. 192; 1876, Novit. Conchol., Abt. 1, **5**, pts. 50-51, p. 21. Pfeiffer, 1879, Nomencl. Helic. Vic., p. 224.

Strophocheilus (*Thaumastus*) *hector* Pilsbry 1895, Man. of Conch., (2) **10**, p. 50.

Thaumastus hector Pilsbry 1902, Man. of Conch., (2) **14**, Classification, p. xxi.

Strophocheilus (*? Megalobulimus*) *hector* Pfeiffer, Bequaert 1948, Bull. Mus. Comp. Zool., Harvard, **100**: 118.

Original description: "T. subimperforata, elongato-ovata, solidula, sub epidermide decidua, fulvida alba; spira conica, apice rotundata; anfr. 6 convexiusculi, summi conferte capillaceo striati, ultimus spiram vix superans, plicato-striatus et obsolete decussatus; columella leviter arcuata, non plicata; apertura subverticalis, acuminato-ovalis, intus albida, nitida; perist. album, marginibus callo albo junctis, dextro subincrassato, brevissime expanso, columellari superne dilatato, adnato. — Long. 71, diam. 35 mill., Ap. 36 mill. longa, 19½ lata."

New Measurements of Adult Holotype

Length	Greatest Width	Aperture Length	Aperture Width	
71 mm.	39 mm.	35 mm.	26 mm.	6 whorls

Specimen examined: Brazil (Miers Coll.), holotype (Brit. Mus., Nat. Hist.).

Remarks. Bequaert (1948, p. 118), who had seen no specimens, was inclined to exclude *hector* from the Strophocheilidae, and Pilsbry (1895, p. 50) placed it in *Thaumastus*. Von Martens (1876), however, suggested that it might be related to *Strophocheilus* (*M.*) *oblongus* (Müller).

Careful examination of the type has convinced us that it is indeed correctly referred to the Strophocheilidae, being by reason of its nepionic sculpture a member of the subgenus *Megalobulimus*. It does not appear, however, to be in any way related to *S.* (*M.*) *oblongus*, the shell being longer and narrower in proportion, much paler and with a white lip. It is furthermore much thinner, the apical sculpture finer, and is covered with a brown periostracum.

S. (*M.*) *hector* would appear to us to be quite distinct from any other species of *Megalobulimus* so far known.

Strophocheilus (Megalobulimus) cocapatensis (Pfeiffer)

Plate 1, figure 2

Bulimus cocapatensis Pfeiffer 1855 (August), Proc. Zool. Soc. London, (for 1855), p. 115 (Cocapata, Bolivia); 1859, Monogr. Helic. Viv., **4**, p. 367; 1868, *Op. cit.*, **6**, p. 11; 1876, *Op. cit.*, **8**, p. 15. Paetel, 1889, Cat. Conch. Samml., 4th ed., **2**, p. 209.

Bulimus (Borus) cocapatensis Pfeiffer 1856 (January), Malak. Blätt., **2**, (for 1855), p. 147. Von Martens, 1860, in Albers, Die Heliceen, 2nd ed., p. 192; 1876, Novit. Conchol., Abt. 1, **5**, pts. 50-51, p. 9. Pfeiffer, 1879, Nomencl. Helic. Viv., p. 224.

Strophocheilus (Borus) cocapatensis Pfeiffer, Pilsbry 1895, Man. of Conch., (2) **10**, p. 20.

Strophocheilus (Borus) cocopatensis Pfeiffer, Pilsbry 1895, Man. of Conch., (2) **10**, p. 12; 1902, *Op. cit.*, (2) **14**, Classification, p. v. Misspelling of *cocapatensis*.

Bulimus corapatensis Pfeiffer, Paetel 1889, Cat. Conch. Samml., 4th ed., **2**, p. 10. Misspelling of *cocapatensis*.

Strophocheilus cocopatensis Pfeiffer, Pilsbry 1930, Proc. Ac. Nat. Sci. Philadelphia, **82**, p. 355. Misspelling of *cocapatensis*.

Strophocheilus (Megalobulimus) cocapatensis Pfeiffer, Bequaert 1948, Bull. Mus. Comp. Zool., Harvard, **100**, no. 1, p. 126.

Original description: "*B.* testa imperforata, ovato-oblonga, solida, minutissime decussata, sub epidermide virenti-fulvida violaceo-carnea; spira convexo-conica, apice obtusa; sutura albida, irregulari; anfr. 5½ superis radiatim costatis et minutissime granulatis, sequentibus peroblique descendentibus, parum convexis, ultimo spiram sub-aequante, basi rotundato; columella recedente, leviter arcuata; apertura subverticali acuminato-ovali, intus margaritacea; perist. incrassato, breviter expanso, marginibus callo nitido junctis, columellari dilatato, adnato. Long. 67, diam. 30 mill."

Measurements of Adult Shells

Length	Greatest Width	Aperture Length	Aperture Width		
67 mm.	33 mm.	31 mm.	21 mm.	5½ whorls.	Holotype
67	33	31	20	5½ whorls.	Paratype
66	33	32	20	5½ whorls.	Paratype

Specimens examined: Cocapata, Bolivia (Bridges Coll.), 3 types from the Cuming Collection (Brit. Mus. [Nat. Hist.]).

Remarks. As pointed out by Bequaert (1948, p. 127), the radially ribbed and minutely granulated nepionic whorls, mentioned in Pfeiffer's original description, are characteristic

of *Megalobulimus,* to which subgenus *S. cocapatensis* undoubtedly belongs. Pilsbry (1930, Proc. Ac. Nat. Sci. Philadelphia, **82**, p. 355), in describing his *S. carrikeri,* infers that it may be related to *S. cocapatensis,* but we are unable to see any justification for this assumption. Bequaert suggests that it is not impossible that *cocapatensis* may be the same as *S. intertextus* Pilsbry, but comparison of a specimen of the latter with Pfeiffer's type has convinced us that they are in no way related.

The shell of *cocapatensis* is imperforate, long, thin and delicate, brown in color, with a very streaky, pink-flushed appearance. The spire is attenuated, the apex pointed, the mouth long and narrow, the aperture brown within, and the outer lip thin, white, slightly reflected. Columella and callus white.

Pfeiffer compared *cocapatensis* with *S. rosaceus,* but, as pointed out by Bequaert, the nepionic sculpture is typical of *Megalobulimus* and is not found in *Chiliborus,* to which subgenus *S. rosaceus* belongs. Pfeiffer later 1856) placed it between "*S. matthewsi*" (= *leucostoma*) and *S. capillaceus* but, as he does not show it as being then in his collection, this opinion would seem of little value.

Strophocheilus (Megalobulimus) capillaceus (Pfeiffer)

Plate 1, figure 3

Bulimus capillaceus Pfeiffer 1855 (July), Proc. Zool. Soc. London, (for 1855), p. 93.

Strophocheilus (*Borus*) *capillaceus* Pfeiffer, Pilsbry 1895, Man. of Conch., (2) **10**, p. 31, Pl. 14, fig. 69.

Strophocheilus (*Megalobulimus*) *capillaceus* Pfeiffer, Bequaert 1948, Bull. Mus. Comp. Zool., Harvard, **100**, p. 120 (full synonymy), Pl. 14, fig. 5.

The type of *S.* (*M.*) *capillaceus* is in the British Museum (Nat. Hist.), from the Cuming Collection. It consists of three syntypes, of which that figured herein is now chosen as lectotype, no holotype having been selected by Pfeiffer.

Measurements of Adult Shells

Length	Greatest Width	Aperture Length	Aperture Width	
64 mm.	38 mm.	37 mm.	24 mm.	5 whorls. Lectotype
60	39	35	30	5 whorls. Syntype
53	33	23	19	5 whorls. Syntype
67	40.5	40.5	22	5½ whorls. Huanaco
69	42	41	21.5	5½ whorls. Santa Ana

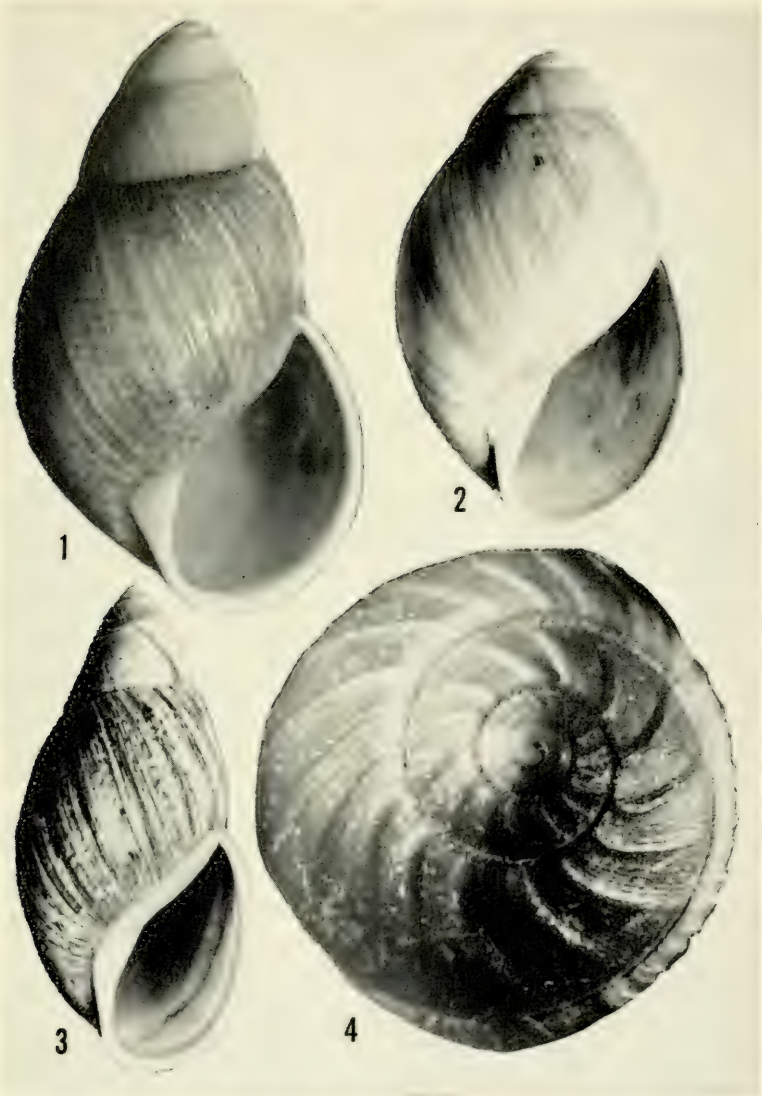

Plate 1

Fig. 1. *Strophocheilus* (*Megalobulimus*) *hoctor* (Pfeiffer). Holotype. nat. size. Fig. 2. *Strophocheilus* (*Megalobulimus*) *cocapatensis* (Pfeiffer). Holotype, nat. size. Fig. 3. *Strophocheilus* (*Megalobulimus*) ***capillaceus*** (Pfeiffer). Lectotype, nat. size. Fig. 4. *Strophocheilus* (*Megalobulimus*) ***maximus indigens*** Fulton. Apical aspect of immature shell, much enlarged.

Specimens examined: "Banks of the River Solimões," Peru (Cuming Collection). Near Santa Ana, Rio Urubamba, Peru, 3500 ft. (W. Weyrauch Coll., in Pain Collection). Huanaco, Peru (Pain Collection).

Remarks. Bequaert (1948, p. 120) has dealt at length with the probable relationships and position in the subgenus of *S. capillaceus*, and gave an excellent figure of it, together with a complete synonymy. To this very full account there is nothing which we can profitably add.

Strophocheilus (Megalobulimus) maximus indigens Fulton

Plate 1, figure 4; Plate 2, figures 5, 6

Bulimus kremnoicus d'Orbigny 1837, Voyage Amér. Méridion., **5**, pt. 3, Moll., p. 300 (in part only: some specimens from Yuracare, Bolivia, the locality given in Explanation of Plates, p. 695, for fig. 3), Pl. 35, fig. 3 only. Not *Helix kremnoica* d'Orbigny 1835.

Strophocheilus (Borus) maximus ? var. *kremnoicus* d'Orbigny, Pilsbry 1895, Man. of Conch., (2) **10**, p. 16, Pl. 5, fig. 28 (copy of d'Orbigny's fig. 3); 1902, *Op. cit.*, (2) **14**, Classification, p. iv.

Strophocheilus (Borus) indigens Fulton 1914, Proc. Mal. Soc. London, **11**, pt. 3, p. 165, fig. (Peru).

Strophocheilus (Megalobulimus) indigens Fulton, Bequaert 1948, Bull. Mus. Comp. Zool., **100**, No. 1, p. 98, Pl. 24, fig. 1 (copy of Fulton's 1914 fig.).

Strophocheilus indigens Fulton, Blume 1952, Arch. f. Mollusk., Frankfurt, **81**, pts. 4-6, p. 105.

Strophocheilus (Borus) kremnoicus subsp. *vestitus* Pilsbry 1926, Proc. Ac. Nat. Sci. Philadelphia, **78**, p. 6 (Bolivia, probably in Dept. Cochabamba), Pl. 2, fig. 7.

Strophocheilus (Megalobulimus) maximus vestitus Pilsbry, Bequaert 1948, Bull. Mus. Comp. Zool., Harvard, **100**: 94, Pl. 19, fig. 4.

Original description: "Shell ovate-oblong, yellowish brown, moderately solid; spire about 13 mm. longer than the aperture; whorls 6½, apex smooth, the second and third whorls with prominent oblique plications, last two volutions polished and apparently smooth, but under the lens are seen to be finely granulated, the granulations being strong on the middle whorls and gradually becoming weaker towards the aperture; the lower whorls have also some irregular and almost obsolete plications; aperture sub-oval, whitish within; peristome thickened and very slightly expanded, white, margins joined by a moderately thickened white callus. Alt. 110, Diam. Maj. 47 mm. The nearest species to this is *S. (Borus) huascari* Tschudi, which is broader, has a wider aperture, a rougher and duller surface, and its apical plications are much finer and closer together than in *indigens*."

MEASUREMENTS OF ADULT SHELLS

Length	Greatest Width	Aperture Length	Aperture Width	Whorls	
135 mm.	57.5 mm.	60 mm.	41 mm.	7	Bolivia: Sacha, Yungas, 800-1500 m. (Bavarian State Mus.)
132	63	59.5	37	7	" "
127	58	56	39	7	" "
128	58	55	31.5	6½	Bolivia (W. Weyrauch Collection)
118.5	61	57.5	40.5	6	Bolivia: Chapare, 400 m. (Bavarian State Mus.)
118	58	56	24	—	Type of *vestitus* Pilsbry
116	48	47	31	6½	Holotype of *indigens*, Peru
101	46	47	26	5½	Bolivia (T. Pain Collection)
100	49	48	27.5	5½	Bolivia (W. Weyrauch Collection)

Specimens examined: Peru, type of *indigens* Fulton (British Museum [Nat. Hist.], No. 1915-1-5-199). Yungas de Palmar, 1200 m., Bolivia (R. Zischka Coll., in W. Blume, T. Pain, and W. Weyrauch Collections).

Remarks. Comparison of the type of *indigens*, together with the shells from Bolivia, with Bequaert's (1948) figure of *vestitus* Pilsbry, leave us in no doubt that they are identical. All show the strong, prominent oblique plications on the second and third whorls, noticeably absent on both the typical *maximus* and the subspecies *huascari*. As pointed out by Bequaert (1948, p. 94), *indigens* (=*vestitus*) is of considerable interest in that it bridges the gap between typical *maximus* and subspecies *huascari* in respect of its relatively wider spire, narrower body-whorl and smaller mouth.

Fulton, who described *indigens* from a unique holotype, did not apparently connect it with *maximus*, although he drew attention to its close resemblance to *huascari*.

Bequaert (1948, p. 94), dealing with *vestitus*, makes no mention of the prominent sculpture, although this is easily recognized in his excellent photograph of the shell he selected as holotype from Pilsbry's type set (Ac. Nat. Sci. Philadelphia No. 138105). Dr. Weyrauch informs us (*in litt.*, 1958) that he considers the elongated shell from Oxapampa, Peru, referred by Bequaert to *vestitus*, to be a typical *maximus* on account of the aperture being much longer than in *indigens* (= *vestitus*). A similar elongated shell from Peru, without more definite locality,

kindly sent by Dr. Weyrauch, shows traces of a dark periostracum and, although much worn about the spire, has the long aperture characteristic of typical *maximus*.

S. (*M.*) *maximus indigens* Fulton has not so far been obtained in Peru by Dr. Weyrauch, but, from the similarity of the fauna of southeastern Peru and northeastern Bolivia, there can be little doubt that *indigens* occurs also in Peru.

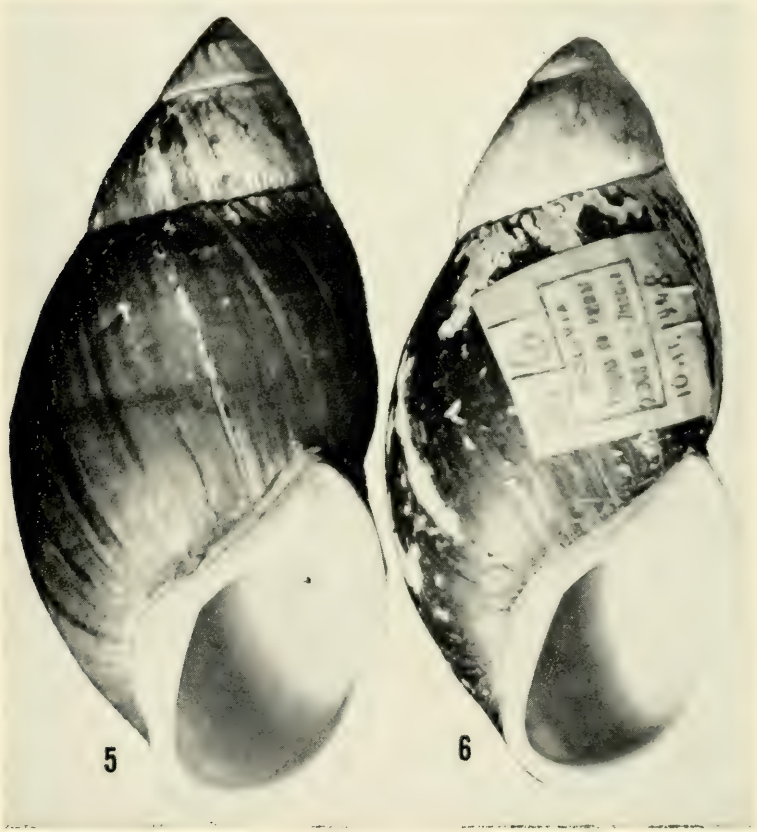

Plate 2

Fig. 5. *Strophocheilus* (*Megalobulimus*) *maximus indigens* Fulton. Holotype, nat. size. Fig. 6. *Strophocheilus* (*Megalobulimus*) *maximus indigens* Fulton. Yungas de Palmar, Bolivia, nat. size.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS. JUNE 15, 1961 NUMBER 139

A NEW SPECIES OF *SPHAERODACTYLUS* FROM NORTHERN HAITI

BY JAMES D. LAZELL

Although the genus *Sphaerodactylus* on Hispaniola is sufficiently diversified and confused to warrant at least a partial revision, the species here described is so remarkably different from any other form that I am confident in naming it at this time.

The new species is named for Mr. Benjamin Shreve of the Museum of Comparative Zoology for his current work on the sphaerodactyls of Hispaniola.

SPHAERODACTYLUS SHREVEI sp. nov.

Type: MCZ No. 62548, Mole Saint Nicolas, Haiti. Coll.: J. Lazell and A. S. Rand, 16 July, 1960.

Diagnosis: The combination of the following characters serves to distinguish this species from any other found in the Antilles: the presence of a highly convex snout as seen from the side (loreal region also somewhat convex); very large keeled dorsal scales beginning at the level of the axilla; and the paravertebral arrangement of these dorsals, producing a middorsal zone not of granules but of small and large, irregularly placed scales.

Description of type. Snout short. Eye nearer tip of snout than ear. Snout, as seen from the side, highly convex. Loreal region also somewhat convex. Rostral large with a partial median cleft. Nostril between rostral, first supralabial, a large supranasal (= internasal) and two small postnasals. A single scale between the supranasals (= internasals), which border the rostral posteriorly. Granular scales on top of snout somewhat larger than interocular or nape scales. Four supralabials, of

about equal length, to the center of the eye, followed by two smaller ones. Four infralabials gradually decreasing in size followed by two abruptly smaller ones. Mental short, wider than long, bordered posteriorly by two postmentals. Supraciliary spine small. Squamation of head and neck granular to the level of the shoulder; at that level a moderately rapid change to large, flattened, heavily keeled dorsals. Twenty-five dorsals from the level of the axilla to the posterior level of the hind limb. Five dorsals in the standard distance. A very ill-defined middorsal zone of smaller *keeled* scales not forming a continuous row but with the large dorsals meeting irregularly along the middorsal line. Middorsals subimbricate or not imbricating, the laterals more distinctly imbricating. Throat scales smooth, granular, juxtaposed. Chest and belly scales larger, smooth, cycloid, broadly imbricate, about nine ventral scales in standard distance. Scales of anterior surfaces of limbs imbricate, cycloid, smooth, somewhat smaller than ventrals. Scales of posterior surfaces of limbs granular, smooth. Digital pads approximately twice as broad as the subdigital lamellae. Ten infradigital lamellae under fourth toe. The type, the only specimen yet collected, lacks the tail. It is a female and the escutcheon therefore cannot be described.

Coloration in life. S. shrevei is a dull-colored animal with a pattern composed of three basic hues — each tending to be unique on an individual scale. There are very irregular dark grey-brown blotches across the dorsum; beginning at the back of the head there are three such markings to the shoulders. There are three more crudely "Y" shaped markings on the body, the most anterior of which bifurcates to the right, the remaining ones bifurcating to the left. There are two small blotches on the right side of the rump and one on the left. The second transverse blotch, on the nape, is broken by a light middorsal line that continues down through the fourth marking and then fades out. The ground color of the dorsum is ash grey. There are scattered over the dorsal surface short transverse series of white or partly white scales — from two to four in a row — that appear to have no correlation whatever with the rest of the animal's pattern. The top of the head is ash grey except for a very irregular, dark, grey-brown blotch on the parietal area. Coming back from the eye are two stripes, one of which runs downward across the cheek; the other nearly connects with the first transverse marking on the back of the head. Not

including the stripe across the cheek, there are five vertical dark markings across the pale labials, the anterior two of which are connected at the edge of the mandible. There are dark streaks on the lateral edges of the chin and throat, the underside of the hind limbs, and across the venter just anterior to the anus. The ventral surface is white; a close examination reveals that on each scale there are tiny black dots. This peppering becomes more noticeable laterally and posteriorly. Along each side of the animal is a line of partially connected, small, dark, grey-brown blotches; just ventral to this row is another composed of widely spaced, single, dark, grey-brown scales. All three of the animal's hues: white, grey and grey-brown, are simply variations in the intensity of speckling on each scale with tiny black or brown dots.

The pattern of the animal bears no resemblance to that of the young or females in the species to which it has been compared, or to any other *Sphaerodactylus* I have seen.

Habitat. The type specimen was taken from a large circular rock pile about two-and-one-half feet deep; this sort of rock pile is the result of removing the debris from a heap of charcoal after burning, and is composed of rocks that vary in size from that of a golf ball to nearly the size of a football. This particular heap was of some age, for even in the arid terrain of Mole Saint Nicolas several fair-sized thornbushes had sprouted up in it. Collecting was very difficult, for any animal uncovered could generally manage to dart back into the pile before the collector could safely ascertain that it was not a scorpion or some other unpleasant handful. In order to get best results we excavated areas through the pile, dividing it up into more manageable smaller piles; this system netted *Celestus*, *Typhlops*, and *Tropidophis*, as well as the type of *Sphaerodactylus shrevei*. Another specimen of apparently the same species escaped, leaving only its tail behind.

Due to the relative inaccessibility of peninsular north-western Haiti it may be some time before additional specimens can be obtained.

Comparisons. From *S. copei*, the only other comparably large-scaled Hispaniolan form, *S. shrevei* differs in the following characters: (1) Snout seen from the side highly convex; (2) No middorsal zone of *granules;* (3) Dorsal scales flatter, not swollen, apt not to imbricate, especially in the middorsal area; (4) Pattern a series of irregular dark dorsal blotches with

a line of often connected smaller blotches along each side; dorsal blotches broken by a light middorsal line anteriorly.

From *S. scaber* of Cuba, *S. shrevei* differs in all the mentioned characters and in snout length, which averages slightly shorter in the Cuban form.

S. samanensis Cochran of the Dominican Republic resembles *S. shrevei* somewhat in squamation but the dorsals are smaller and the ventrals larger. There are no smaller middorsal scales and the pattern is very different.

S. shrevei differs from *S. becki* of Navassa again in the absence of a middorsal zone of granular scales and in the flatness of the dorsal scales, which are rounded, swollen, and rather tubercular in *S. becki.*

Two Jamaican forms, *S. richardsoni* and *S. parkeri,* occasionally possess dorsal squamation similar to that of *S. shrevei* in that while there is no middorsal zone of granules there may be small scales irregularly scattered along the middorsal line, but in general the arrangement of the scales is much more regular and not of a paravertebral nature. From both of these species *S. shrevei* differs in the following characters: (1) Snout seen from the side highly convex; (2) Head *granules* extending posteriorly to level of axilla instead of just onto nape; (3) No enlarged, clearly defined canthal scale; (4) Pattern and coloration.

From *S. parkeri* it differs also in having only a single small scale between the internasals.

There is a vaguer resemblance to *S. shrevei* in some Lesser Antillean forms. *S. vincenti* and *S. microlepis,* for example, show a tendency towards reduction in size of the middorsal scales, but in these forms the pattern of squamation tends to be very regular and the scales are much smaller.

The new species has been compared with these forms largely because there are apparently no closer ones, although it bears little resemblance to any of them. Its relationships at the moment are not at all clear.

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TABLE 1

Comparison of the snout length ratios of six species of *Sphaerodactylus*. The ratio is obtained by dividing the standard distance (i.e., the distance from the center of the eye to the tip of the snout) into the distance from the center of the eye to the ear opening. The higher the figure obtained the shorter the snout.

	Specimens	*Mean Value*	*Range*
S. richardsoni	5	.72	.67- .81
S. parkeri	3	.76	.73- .78
S. copei	10	.76	.70- .80
S. shrevei	1	.80	-
S. scaber	6	.82	.71- .92
S. becki	4	.90	.78-1.00

BREVIORA

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A PRELIMINARY REVIEW OF THE NEARCTIC SPECIES OF SIEROLOMORPHA (HYMENOPTERA)

BY HOWARD E. EVANS

In the course of collecting Bethylidae and examining material in various museums, I have encountered a good many specimens of the curious bethylid-like genus *Sierolomorpha* Ashmead. Some of these specimens are so different from the type, *ambigua*, for a long time the only known species, that it seems desirable to provide names for them. Krombein (1951, U. S. Dept. Agri. Monogr. 2, p. 748) has already pointed out that there appear to be several species in North America. The present paper does not pretend to be an exhaustive treatment of this genus. Names are provided for several of the more distinctive species, but before a definitive revision is possible more collecting must be done and more detailed studies made of structural details and their variation.

Actually, *Sierolomorpha* is not a bethylid or even especially close to the Bethylidae. Schuster (1949, Ent. Amer., 29: 124) is correct in pointing out its close similarity to certain Mutillidae and Tiphiidae, and the arrangement in the Synoptic Catalog (Krombein, 1951, *op. cit.*), in which the genus is placed in a monogeneric family between the Tiphiidae and Mutillidae, is probably the best that can be achieved at present. *Sierolomorpha* is related to the most primitive Scolioidea, and may not be far from the stock which gave rise to the Bethylidae. However, in virtually all structural details it stands very much closer to the Tiphiidae than to the Bethylidae.

Only one species of the genus, *hospes* Perkins, has been described from outside the Nearctic region (from Hawaii). Krombein has suggested that this species may have been introduced from North America. In the collection of the U. S. National Museum there is a single male of an undescribed species from

Panama. I have seen no other specimens from outside the United States and Canada.

The most useful structures for the separation of species in this genus appear to be the antennae, especially the tyloides of the male (Figs. 1-6), the propodeum, and the first two abdominal tergites. There seems to be little variation within the genus with respect to the mandibles, clypeus, and most details of the thorax including the legs and wing venation. I have therefore made little mention of these structures in my descriptions. I have studied the male terminalia of selected specimens and found some minor variation, particularly in the volsellar cuspis. However, the differences are so slight and subtle that further study to determine the extent of individual variation did not seem warranted. I have therefore made no mention of characters of the terminalia in the keys and descriptions.

The following abbreviations are used for the museums and private individuals that supplied material for this study: AMNH, American Museum of Natural History, New York; CIS, California Insect Survey, Berkeley; CNC, Canadian National Collections, Ottawa; HKT, Henry K. Townes, Ann Arbor, Michigan; MCZ, Museum of Comparative Zoology, Cambridge, Mass.; UCD, University of California at Davis; USNM, U. S. National Museum.

Key to Species

Females [1]

1. Abdomen with the constriction between the first two tergites strong, the first tergite with a weak to strong apical transverse depression which is longitudinally striate; propodeum with a moderately wide median groove which is irregularly margined by carinae 2

   Abdomen with the constriction between the first two tergites weak, first tergite smooth, not depressed or striate apically; propodeum with median groove absent or linear and not margined as above 3

2. Legs beyond the coxae bright yellowish-brown; basal segments of antennae suffused with light yellowish-brown; notauli strongly diverging anteriorly (Florida and Arizona to Alberta, Ontario, and Massachusetts) . . . . . *canadensis* (Provancher)

[1] The females of two species, *apache* and *brevicornis*, are unknown.

Legs brown except front tibiae and tarsi yellowish-brown; antennae brown, sometimes weakly suffused with paler brown on sides of basal segments; mesoscutum rather flat, notauli weakly diverging anteriorly (California, Arizona, and Colorado to Saskatchewan and Yukon) . . . . . *nigrescens* n. sp.

3. Front, pronotum, and mesopleura with strong punctures; pro- and mesonota bright rufocastaneous (Arizona) . . . *bicolor* n. sp.

Front, pronotum, and mesopleura with only minute, widely spaced punctures; thorax entirely black (Georgia to Connecticut and Kansas) . . . . . *similis* n. sp.

Males

1. Abdomen with the constriction between the first two tergites strong, the first tergite with a weak to strong apical transverse depression which is longitudinally striate; tyloides present on antennal segments seven through ten, short and rather prominently projecting (Figs. 1, 2); propodeum as in female (see couplet 1 of key to females) 2

Abdomen with the constriction between the first two tergites weak or absent, the first tergite smooth, not depressed or striate apically; tyloides not present on antennal segment seven or, if so, very long and low on segments eight and nine 3

2. Tibiae and tarsi mostly or entirely light yellowish-brown in most specimens; temples rather short, as seen from above much shorter than eyes (Florida and Arizona to Alberta, Ontario, and Massachusetts) . . . *canadensis* (Provancher)

Legs brown except front tibiae (sometimes also front tarsi and middle tibiae) light yellowish-brown; temples strongly developed, as seen from above nearly as wide as the eyes (California, Arizona, and Colorado to Saskatchewan and Yukon) . . . . . *nigrescens* n. sp.

3. Antennae extremely short and compact, segment eleven about 1.2 X as long as thick, segment thirteen about 1.5 X as long as thick; tyloides present on antennal segment eleven (Fig. 3); head extremely broad, about 1.25 X as wide as high (South Carolina) . . . . . *brevicornis* n. sp.

Antennae elongate, segment eleven about twice as long as thick, segment thirteen much more than twice as long as thick; tyloides not present beyond segment ten; head 1.1-1.2 X as wide as high 4

4. Ocelli distinctly enlarged (diameter of anterior ocellus about .22 X minimum width of front); tyloides present on antennal segments seven through ten (Fig. 6); front with a strong median groove in front of anterior ocellus (Arizona) . . . . . *apache* n. sp.

   Ocelli not enlarged (diameter of anterior ocellus less than .2 X minimum width of front); tyloides present on segments eight through ten (Figs. 4, 5); front with a weak median impression if any 5

5. Punctures of front moderately strong; tyloides rather short (Fig. 5); middle and hind tibiae and tarsi dull brown (Arizona) . . . . . ? *bicolor* n. sp.

   Punctures of front very weak; tyloides elongate (Fig. 4); all tibiae and tarsi light yellowish-brown (Georgia to Connecticut and Kansas) . . . . . *similis* n. sp.

Sierolomorpha bicolor new species

Holotype. — ♀, **ARIZONA:** Southwestern Research Station, 5 mi. W. of Portal, Cochise Co., 9 August 1959, 5400 feet elevation (H. E. Evans) [MCZ].

Description of type female. — Length 5.8 mm., length of fore wing 4.3 mm. Head black; pronotum, mesoscutum, and scutellum wholly bright rufo-castaneous; remainder of thorax and propodeum black; abdomen very dark brown, approaching black basally; mandibles light brown, darker basally and apically; clypeus suffused with reddish-brown apically; scape black, flagellum dark brown, outer side of apical segments paler; legs dark brown except front and middle tibiae and all tarsi light brown; fore wing lightly, uniformly infuscated, veins and stigma dark brown. First four antennal segments in a ratio of about 12:5:7:9, segment three 1.4 X as long as thick. Front strongly polished, punctures small but rather strong; spacing of punctures rather irregular, those on the sides being mostly rather close, often not much more than their own diameters apart, those on the middle of the front rather sparse; temples also with distinct punctures. Head subcircular in anterior view, vertex evenly rounded off a short distance above eye tops; inner orbits subparallel, minimum width of front about .9 the eye height. Ocelli small, in a broad triangle, the front angle greater than a right angle; postocellar line slightly exceeding ocello-ocular line. Thoracic dorsum strongly polished, non-alutaceous; pronotum with strong, widely spaced punctures; mesoscutum with

a very few punctures on the sides, impunctate medially. Propodeum strongly polished medio-basally, elsewhere slightly roughened by obscure punctures; median line weakly impressed. Mesopleurum polished and with well-defined punctures. First abdominal tergite without a subapical depressed and striate band, completely smooth; constriction between first and second tergites weak; abdomen rather strongly hirsute beyond segment three.

Male (assigned here tentatively). — **ARIZONA:** Cochise Stronghold, Dragoon Mts., 4850 feet elevation, oak-juniper zone, 2 July 1947 (Werner & Nutting) [Univ. Arizona].

Description of male. — Length 5 mm., length of fore wing 4.8 mm. Head and thorax entirely black, abdomen dark brown; apical half of mandibles light brown; antennae wholly dark brown; legs wholly dark brown except front tibiae and tarsi bright yellowish-brown; wings subhyaline. First four antennal segments in a ratio of about 20:8:13:20, segment three 1.5 X as long as thick, segment four 2.2 X as long as thick, this segment typical of the remaining segments except the last; segments eight through ten each with a short, rather weak longitudinal polished ridge (Fig. 5). Front polished, wholly covered with small but well-defined punctures which are separated by scarcely more than their own diameters; vertex and temples more weakly punctate; front somewhat impressed along the inner orbits and beside the posterior ocelli, faintly impressed medially. Minimum width of front approximately equal to eye height; ocelli in a broad, flat triangle, postocellar and ocello-ocular lines subequal; ocelli of moderate size, diameter of anterior ocellus .18 X minimum width of front. Pronotum short, shining and with dense, rather weak punctures. Mesonotum shining, rather sparsely and weakly punctate. Propodeum polished, impunctate, and nonalutaceous over most of its surface. Mesopleurum polished, densely but weakly punctate. First abdominal tergite smooth, without a subapical depressed and striate band.

Remarks. — The type female was taken on the ground beneath oak trees in dry, open forest. The male associated with it tentatively was apparently taken in the same type of forest and at nearly the same altitude.

Sierolomorpha apache new species

Holotype. — ♂ **ARIZONA:** 3-5 mi. SW of Apache, Cochise Co., 8 August 1959, about 4300 feet elevation (H. E. Evans, on *Baccharis glutinosa*) [MCZ].

Description of type male. — Length 4.5 mm., length of fore wing 4.0 mm. Entire body dark brown, the head nearly black; mandibles light brown; antennae uniformly light brown; legs dark brown except tibiae and tarsi light brown, the front tibiae a rather bright yellowish-brown; wings hyaline. First four antennal segments in a ratio of about 15:9:13:17, segment three 1.6 X as long as thick, segment four 2.0 X as long as thick, segment eleven 2.1 X as long as thick; segments seven through ten each with a weak longitudinal polished ridge (Fig. 6). Front polished, with weak, scattered punctures, with a very strong median groove extending downward from the anterior ocellus; eyes large and prominent, inner orbits subparallel below; head about 1.2 X as wide as high. Minimum width of front 1.07 X eye height; ocelli large, diameter of anterior ocellus .22 X minimum width of front; postocellar line 1.15 X ocello-ocular line. Pronotum short, shining, weakly punctate. Mesonotum strongly shining, obscurely punctate. Propodeum in large part strongly polished, median area without ridges or other sculpturing except for a simple carina on the posterior third. Mesopleurum shining, obscurely punctate. Abdomen with scarcely any indication of a constriction between the first two segments either dorsally or ventrally; first tergite without an apical striate depression.

Remarks. — This striking specimen was taken on vegetation in the daytime, although the large ocelli suggest that the species may be nocturnal or crepuscular. The locality was a dry wash in an area of desert grassland.

Sierolomorpha similis new species

Holotype. — ♂, **MARYLAND:** Takoma Park, 22 Sept. 1945 (H. & M. Townes) [HKT].

Description of type male. — Length 4.4 mm., length of fore wing 4.1 mm. Body dark brown, head and thorax almost black; mandibles light brown; antennae uniformly dark brown; coxae dark brown, femora medium brown, paler apically, tibiae and tarsi yellowish-brown; wings lightly tinged with fuscous. First four antennal segments in a ratio of about 19:10:13:18, segment three almost twice as long as thick, segments four and eleven about 2.1 X as long as thick; tyloides in the form of low carinae on segments eight through ten, the carina on eight extending for much of the length of the segment, the others slightly shorter (Fig. 4). Front strongly polished, with small, rather evenly distributed punctures which are separated by 1-2 X their own

diameters; median line of front weakly impressed. Head 1.12 X as wide as high, subcircular in anterior view, temples only moderately developed, contracted immediately behind eyes. Inner orbits convergent below, minimum width of front subequal to eye height; ocelli of moderate size, diameter of anterior ocellus .17 X minimum width of front; postocellar line 1.1 X ocello-ocular line. Pronotum strongly shining, with a great many minute punctures. Mesoscutum strongly shining, obscurely punctate, notauli strong, nearly reaching anterior margin. Dorsal surface of propodeum shining, with a linear median groove. Mesopleurum strongly polished and nearly impunctate. First abdominal tergite polished, smooth, with no evidence of a transverse apical depression; second tergite with a narrow transverse basal impression, so that there is vague evidence of a constriction between the first two tergites.

Allotype. — ♀, Kearny, New Jersey, 9 Sept. 1935 (C. W. Funaro) [AMNH].

Description of allotype female. — Length 5.1 mm.; length of fore wing 3.6 mm. Head and thorax dark brown, abdomen medium brown; mandibles and apical half of clypeus light yellowish-brown; antennae dark brown except scape and pedicel suffused with yellowish-brown and flagellum light brown beneath; coxae brownish but legs otherwise wholly bright yellowish-brown; wings lightly tinged with fuscous. First four antennal segments in a ratio of about 23:10:11:15, segment three 1.5 X as long as thick, segment eleven 1.7 X as long as thick. Front strongly polished, punctures small and widely separated. Head subcircular in anterior view, about as wide as high; inner orbits subparallel, minimum width of front subequal to eye height. Ocelli small, in a broad triangle; postocellar line subequal to ocello-ocular line. Pronotum polished, with scattered small punctures. Mesonotum impunctate, notauli strong on posterior .8 of mesoscutum, diverging and attenuate anteriorly. Propodeum mostly smooth and shining, with a very thin median groove which posteriorly is paralleled by some irregular carinae. Mesopleurum convex, smooth and shining. Abdomen fusiform, depressed; first tergite smooth and polished, with no evidence of a transverse apical impression; second tergite barely depressed basally.

Paratypes. — **CONNECTICUT:** 1 ♀, Bank of Conn. River, East Hartford, 2 Sept. 1947 (H. E. Evans) [MCZ]; **NEW YORK:** 1 ♀, Sea Cliff, Long Island [MCZ]; **MARYLAND:** 3 ♂ ♂, Takoma Park, same data as type [MCZ, HKT]; **WEST**

VIRGINIA: 1 ♂, Shaver's Fork, Tucker Co., Oct. 1938 (G. E. Wallace) [Carnegie Mus.]; **SOUTH CAROLINA:** 1 ♂, Greenville, Oct. 1952 (L. & G. Townes) [HKT]; **GEORGIA:** 1 ♂, Macon, 1 Dec. 1923 (T. H. Hubbell) [USNM]; **KANSAS:** 3 ♂♂, Manhattan, Sept., Nov. (D. A. Wilbur, T. F. Winburn) [Kansas State Univ.].

Variation. — The two female paratypes are very similar to the allotype. The Connecticut specimen has the basal two antennal segments bright amber-colored, contrasting strongly to the flagellum; the Long Island specimen is without a head. The males show a small amount of size variation; the smallest specimen (Manhattan, Kansas) has a fore wing measuring 3.6 mm., the largest (Takoma Park, Md.) has a fore wing measuring 4.4 mm. The Kansas specimens tend to have the body (especially the abdomen) slightly paler in color, but otherwise little variation in color or body sculpture can be noted. In most specimens the postocellar line is subequal to the ocello-ocular line, and in one specimen it is somewhat shorter.

Sierolomorpha brevicornis new species

Holotype. — ♂, **SOUTH CAROLINA:** Greenville, 21 Sept. 1952 (L. & G. Townes) [HKT].

Description of type male. — Length 3.4 mm., length of fore wing 2.7 mm. Body dark brown, head almost black; mandibles light brown on apical half; antennae dark brown, very slightly paler beneath; legs dark brown except front tibiae and tarsi light yellowish-brown; wings hyaline. First four antennal segments in a ratio of about 12:6:7:8, segment three 1.1 X as long as thick, apical segment unusually short and thick, about 1.5 X as long as thick; tyloides present on segments nine through twelve, but rather small (Fig. 3). Front strongly polished, punctures minute, shallow; median line strongly impressed in front of anterior ocellus. Head very broad, 1.25 X as wide as high; front broad, its minimum width .61 X width of head, 1.18 X height of eye; ocelli small, diameter of anterior ocellus .14 X minimum width of front; postocellar line very slightly greater than ocello-ocular line. Vertex forming a broad, even arc above the eye tops; temples moderately developed, in dorsal view about two-thirds as wide as eye. Pro- and mesonota shining, obscurely punctate; notauli strong, complete, diverging anteriorly. Propodeum mostly smooth and polished, median line weakly grooved, ecarinate. Mesopleurum strongly shining, obscurely

punctate. Venation differing from that of other species only in having the second recurrent and second transverse cubital veins very weakly indicated and the margin cell somewhat more rounded apically. First two abdominal segments without a constriction between them, first tergite smooth and polished, without a striate depression along its apical margin.

SIEROLOMORPHA NIGRESCENS new species

Holotype. — ♂, **WASHINGTON:** Olympia [USNM].

Description of type male. — Length 4.4 mm., length of fore wing 3.7 mm. Body dark brown, almost black; mandibles light brown; antennae uniformly dark brown; legs dark brown except front tibiae bright yellowish-brown; wings lightly tinged with fuscous. First four antennal segments in a ratio of about 20:8:11:16, segment three only 1.3 X as long as thick, segment four about 1.7 X as long as thick; segments seven through ten each with a short but rather strong longitudinal ridge (Fig. 1). Front strongly polished, with minute punctures which are rather close together below, much more widely scattered above; median line of front weakly impressed. Head about 1.15 X as wide as high, rather thick, seen from above with the temples nearly as thick as the eyes, the head across the temples nearly as wide as across the eyes. Inner orbits subparallel below; minimum width of front 1.13 X height of eye; ocelli small, diameter of anterior ocellus .14 X minimum width of front; postocellar line subequal to ocello-ocular line. Pronotum strongly shining, obscurely punctate. Mesoscutum polished and nearly impunctate, with very strong notauli which diverge slightly anteriorly and do not quite reach the anterior margin. Propodeum with two median carinae between which it is somewhat grooved, disc otherwise with weak and irregular sculpturing, somewhat shining. Mesopleurum shining and with very small punctures. Abdomen with a strong constriction between the first two segments: first tergite depressed along the posterior margin, second tergite along its anterior margin, both depressions with longitudinal striations.

Allotype. — ♀, **WASHINGTON:** Seattle [USNM].

Description of allotype female. — Length 4.5 mm., length of fore wing 3 mm. Head and thorax dark brown, abdomen medium brown, somewhat darker apically; mandibles and apical half of clypeus light brown; antennae dark brown, suffused with lighter brown on the sides of the basal flagellar segments; legs dark brown except front tibiae bright yellowish-brown; wings lightly

tinged with fuscous. First four antennal segments in a ratio of about 22:9:9:13, segment three 1.2 X as long as thick. Front strongly polished, punctures minute and widely scattered. Head subcircular in anterior view, very slightly wider than high; inner orbits subparallel, minimum width of front 1.16 X height of eye. Ocelli small, in a broad triangle; postocellar line 1.1 X ocello-ocular line. Pro- and mesonota polished, obscurely punctate; notauli deeply impressed, diverging only slightly anteriorly, terminating well short of anterior margin of mesoscutum. Propodeum and mesopleurum as described for male. Abdomen fusiform, shining; first tergite with a transverse apical depression which is strongly longitudinally striate.

Paratypes. — **WASHINGTON:** 1 ♂, same data as type [USNM]; 1 ♀, Almota, 24 June 1911 [MCZ]; **IDAHO:** 1 ♂, Harvard, 24 June 1935 (J. M. Beck) [USNM]; 2 ♂♂, Moscow, June, July [USNM]; 1 ♂, Nezperce, 18 June 1935 (J. M. Beck) [USNM]; **UTAH:** 1 ♂, Uinta Co. (G. E. Wallace) [Carnegie Mus.]; **CALIFORNIA:** 1 ♂, Sagehen, nr. Hobart Mills, 21 June 1954, on *Phacelia humilis* (P. D. Hurd) [CIS]; 1 ♂, Carnelian Bay, Lake Tahoe, 17 June 1958 (R. M. Bohart) [UCD]; 4 ♂♂, Pasadena, April 1944 (K. W. Cooper) [USNM]; 1 ♂, Rio Linda, Sacramento Co., 19 May 1958 (Light trap, Jack Fowler) [UCD]; 1 ♂, Donner Pass, 1 Aug. 1948 (H., M., G. & D. Townes) [HKT]; 1 ♂, Cisco, 31 July 1948 (H., M., G. & D. Townes) [HKT]; **ARIZONA:** 1 ♂, North Rim, Grand Canyon, 29 July 1954 (H. E. Evans) [MCZ]; **COLORADO:** 1 ♀, Waldo Canyon, 30 June 1916 (W. D. Edmonston) [USNM]; **SASKATCHEWAN:** 1 ♂, Saskatoon, 30 June 1950 (A. R. Brooks) [CNC]; **ALBERTA:** 1 ♀, 30 ♂♂, Onefour, 3 June 1956 (O. Peck) [CNC]; **YUKON:** 1 ♀, Whitehorse, 4 July 1948 (Mason and Hughes) [CNC].

Variation.— The four female paratypes are very similar to the allotype in color and in all important structural details; the length of the fore wing varies from 3 to 3.6 mm. The males exhibit much size variation, the smallest (Donner Pass, Calif.) having the fore wing only 2.2 mm. long, the largest (Rio Linda, Calif.) having the fore wing 4.5 mm. long. There is little color variation except that the front tibiae are dull brown in a few specimens, while in others the middle tibiae are light yellowish-brown like the front tibiae. In most specimens the postocellar and ocello-ocular lines are subequal.

Remarks. — This species is very similar to *canadensis* and may represent no more than a western race of that species. However, there seems to be some overlap of the ranges in Arizona and in western Canada.

Sierolomorphia canadensis (Provancher)

Photopsis canadensis Provancher, 1888, Add. Corr. Faune Ent. Canada, Hymen., p. 410 [Type: ♂, Ottawa, Canada (Harrington)].

Sierola (?) *ambigua* Ashmead, 1893, Bull. U. S. Nat. Mus., 45: 56 [Type: ♂, Brookings, So. Dakota (Coll. Ashmead) (USNM, no. 56018)].

Mutilla tertia Dalla Torre, 1897, Cat. Hymen., 8: 91 (new name for *canadensis*, preoccupied in *Mutilla*).

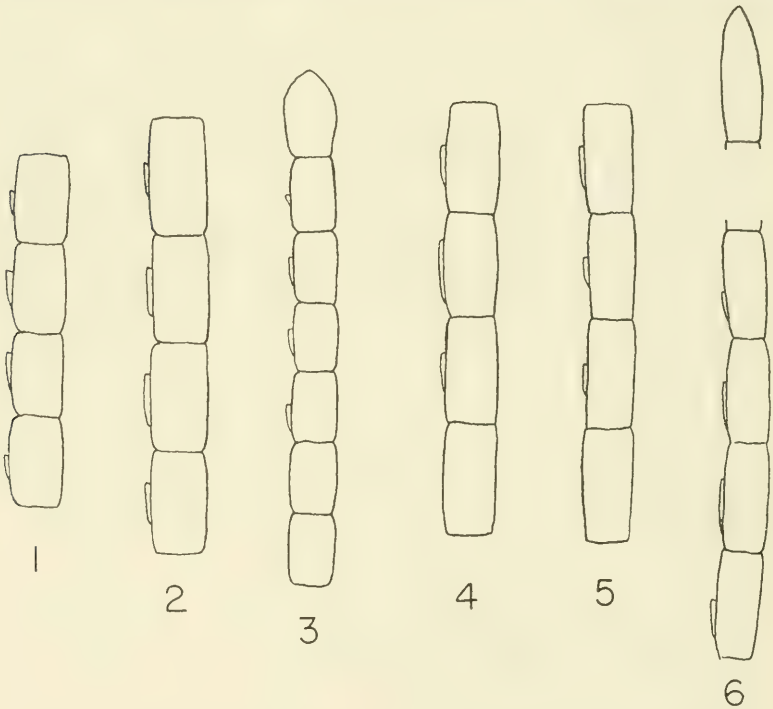
Sierolomorpha ambigua Ashmead, 1903, Canad. Ent., 35: 42.

Sierolomorpha canadensis Krombein, 1951, U. S. Dept. Agri., Agri. Monogr., 2: 749.

Remarks. — Provancher's *canadensis* was transferred to this genus by Krombein on the advice of R. M. Schuster, who stated that a specimen in the University of Minnesota collection which had been compared with Provancher's type was found to be the same as *ambigua* Ashmead. I have not seen Provancher's type, but his description does indeed seem to fit this species rather well. The following statement in particular makes it clear that his name applies to a species (such as this one) with a rather marked constriction between the first two abdominal tergites: "la suture entre les segments 1 et 2 enfoncée et crénelée." Unfortunately, the abdomen of the type of *ambigua* is missing, but my interpretation of Ashmead's species is based upon a topotype which agrees closely in all details regarding the head and thorax, including the characteristic sculpture of the median line of the propodeum. It seems to me best to consider *canadensis* and *ambigua* synonyms, with the former having priority over the more widely used name *ambigua*. I admit the possibility that I may be confusing more than one species here. However, specimens from the northern tier of states and from Canada show no undue amount of variation, and I consider it very doubtful that Ashmead and Provancher had different species before them.

Distribution. — This species occurs widely over eastern North America, ranging from Florida, Texas, and Arizona to Alberta, Ontario, and Massachusetts. I have seen specimens from the following localities: **MASSACHUSETTS:** Waltham, June; **CONNECTICUT:** Lyme, June; **NEW YORK:** Oneonta, Ithaca, Riverhead, L. I., Northwest, L. I., June-Aug.; **PENNSYLVANIA:** Hummelstown, May; **MARYLAND:** Bowie, Takoma Park, May-July; **VIRGINIA:** Rosslyn, Great Falls, Fredricksburg, May-June; **NORTH CAROLINA:** Highlands, Wallace, Pink Beds,

June-July; **GEORGIA:** Tifton, Valdosta, May; **FLORIDA:** Ormond, Osceola Co., Volusia Co., Brevard Co., Dec.-Jan.; **OHIO:** Columbus, June; **MICHIGAN:** Ann Arbor, Erie, Livingston Co., June-Aug.; **ILLINOIS:** Champaign; **IOWA:** Sioux City, Ames, June; **ALBERTA:** (no further data); **NORTH DAKOTA:** Bottineau, Aug.; **SOUTH DAKOTA:** Brookings, June-July; **KANSAS:** Lawrence, Manhattan, Pottawatomie Co., Geary Co., May-July; **LOUISIANA:** Tallulah; **TEXAS:** Sealy, Victoria, May, Nov.; **NEW MEXICO:** Mesilla Park, Sept.; **ARIZONA:** Springerville, July.



Figs. 1-6. Middle antennal segments of males of six species of *Sierolomorpha*. In each case the first segment shown (at the bottom) is segment seven. These figures are somewhat diagrammatic, as the tyloides normally form a somewhat twisted series, here shown as a straight series; furthermore, the tyloides are normally somewhat obscured by setulae, here omitted. Fig. 1 — *S. nigrescens* n. sp., segments 7-10; Fig. 2 — *S. canadensis* (Prov.), segments 7-10; Fig. 3 — *S. brevicornis* n. sp., segments 7-13; Fig. 4 — *S. similis* n. sp., segments 7-10; Fig. 5 — *S. bicolor* (?) n. sp., segments 7-10; Fig. 6 — *S. apache* n. sp., segments 7-10 and 13.

BREVIORA

Museum of Comparative Zoology

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THREE NEW TOADS FROM SOUTH AMERICA: *BUFO MANICORENSIS, BUFO SPINULOSUS ALTIPERUVIANUS* AND *BUFO QUECHUA*

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INTRODUCTION

In the course of a general study of the Neotropical Bufonidae, I received some material from the British Museum (Natural History) (BMNH), the American Museum of Natural History (AMNH), the Carnegie Museum (CM) and the Museum of Zoology at the University of Michigan (MZUM) which included the new forms described below.

One of these is a quite different form of *Bufo* from the State of Amazonas, Brasil; another is a subspecies of *Bufo spinulosus* from the Department of Oruro, Bolivia, and the last a new species of the *Bufo ockendeni* group from the Department of Cochabamba, Bolivia.

BUFO MANICORENSIS sp. nov.

Type. BMNH 1898, 3.10.1, adult male, Manicoré, Rio Madeira, State of Amazonas, Brasil.

Description. Head elongate and sharp. Rostrum nearly vertical. Nostrils on a prominence, elongate and oblique. Cephalic crests well marked, with smooth or somewhat rippled borders. Subnasal crests visible. Canthal crests nearly convergent. Maxillary crests somewhat expanded. Preorbital crests slightly sloping posterolaterally. Postorbital crests sloping anterolaterally, close to the anterior border of the tympanum. Suborbital crests not expanded, rather distant from the lower border of the eye.

Supraorbital crests somewhat raised; interorbital space very narrow and concave, with granules in the parietal region. Parietal crests elongate and oblique, forming an angle with the supraorbital crests. Orbitotympanic crests short but distinct. Greatest diameter of eye, 6 mm. Vertical diameter of tympanum, 3 mm. Tympanum on an outward sloping plane. Paratoids subtriangular with indistinct borders, with their long axis oblique mediolaterally, with flat dorsal granules. One subgular vocal sac. Dorsum with flat granules. Belly with the larger granules on abdominal region. Limbs with dorsal conical granules. Without interdigital membrane in the hand; 1st and 2nd fingers subequal; subarticular tubercles double on fingers 2 and 3; two carpal tubercles, the inner one smaller, elliptic and somewhat salient, the outer larger and rounded. Subarticular tubercle double on toe 4; interdigital membrane in the toes to near the tip of the digits, but in toe 4 basal and prolonged as a serrated cutaneous fringe; two metatarsal tubercles small but elongate, the inner more salient; tarsal fringe absent. Dorsal coloration light brown, with some darker spots, not well marked. Belly light.

Dimensions. Head and body 50 mm. Head length 12.5 mm. Head width 17 mm. Head height 5.5 mm. Interorbital space 2.5 mm. Elbow to the third finger 21 mm. Femur 18 mm. Tibia 16 mm. Heel to the fourth toe 25.5 mm. Foot 17 mm.

Diagnostic features. Bufo manicorensis differs from all other Neotropical toads; the shape of the head and cephalic crests recall certain Asiatic forms. In the Neotropical area the nearest species is *Bufo intermedius* Günther, but this is distinguished by the well marked parietals and preorbitals, the interorbital space narrower than the upper eyelid, the distinct tympanum, and by the paratoids which are not elliptical and are separated from the eye by the orbitotympanic crests. The new species is not as close to *Bufo vallicepS* Wiegmann and differs from that species in having less prominent cephalic crests, the interorbital space narrower, double subarticular tubercles on the foot and no lateral granules in a row continuing the paratoids posteriorly.

Material studied. BMNH 1898, 3.10.1 (1 specimen), Manicoré, Rio Madeira, Brasil, B. Piffard.

Bufo spinulosus altiperuvianus subsp. nov.

Type. AMNH 14418, adult female, Challapata, Department of Oruro, Bolivia.

Description. Head very short and wide. Loreal region sloping

outward. Rostrum vertical. No cephalic crests, excepting maxillaries; canthus rostralis thick. Interorbital space granular. Tympanum sloping out. Paratoids well marked and rounded, continued laterally by large granules (each granule with many horny points). Two types of dorsal granules: the larger with one central horny point and many others around it, the smaller with only one horny point. Larger granules on abdominal region. First finger longer than second; subarticular tubercles on the fingers, double or semidivided; palmar outer tubercle larger and rounded, inner smaller and elongate. Interdigital membrane of the foot basal but prolonged as a fringe on the toes; subarticular tubercles on the toes, simple or sometimes double; two metatarsal tubercles, the inner more salient; a thick tarsal fringe.

Dimensions. Head and body 80 mm. Head length 17 mm. Head width 30 mm. Head height 11 mm. Interorbital space 6 mm. Upper eyelid width 6 mm. Eye 7 mm. Tympanum 3.5 mm. Paratoid 9 mm. by 8.5 mm. Elbow to the third finger 38 mm. Femur 36 mm. Tibia 30 mm. Heel to the fourth toe 50 mm. Foot 35 mm.

Paratype. AMNH 14417, Choro, Bolivia, adult female 82 mm.

Distribution. The two localities of the material studied, Challapata and Choro, are in the Department of Oruro, Bolivia; the type locality is at 3700 metres altitude.

Diagnostic features. According to Vellard (1959), there are six subspecies of *Bufo spinulosus*: *B. s. spinulosus, B. s. arequipensis, B. s. limensis, B. s. trifolium, B. s. flavopictus* and *B. s. orientalis. B. s. altiperuvianus* adds a seventh.

Bufo s. altiperuvianus differs from *B. s. spinulosus,* the Bolivian subspecies structurally and geographically closest (Department of La Paz) in having the head shorter, not so distinct from the body; the loreal region sloping more laterally; tympanum larger; paratoids larger and more rounded. Capurro (1950: 11) has cited *B. spinulosus* from Tarapacá Province, Chile (west of Oruro Department, on the other side of the Cordillera Occidental), but specimens of this provenance that I examined at the Chicago Natural History Museum are different from the form here described.

Remarks. I name this subspecies after the old Spanish name, Alto Perú, of the region from which it derives.

Material studied. AMNH 14418 (1 specimen) Challapata, Bolivia. AMNH 14417 (1 specimen) Choro, Bolivia.

BUFO QUECHUA sp. nov.

Type. CM 4225, adult female, Incachaca, 2500 m., Department of Cochabamba, Bolivia.

Description. Head triangular, widest at the angle of the mouth; loreal region sloping outward. Maxillary border marked; canthus rostralis thick; supraorbital crest absent; parietal crest visible; orbitotympanic crest thick; one rostral-internasal crest more or less marked. Tympanum not visible. Paratoids approximately elliptic, dorsally smooth. Body dorsally with sparse large granules, but with abundant small granules. One lateral row of granules, continuing the paratoids, each granule with a large central papilla and smaller papillae around it; below the row, lateral granules of the same type. Belly with abundant conical and simple granules. Elongate limbs, with conical granules dorsally. First finger longer than second; fingers free, borders with small conical granules; subarticular tubercles generally simple, but double on the third finger; outer palmar tubercle large and rounded, inner one smaller and elongate. Tarsal fringe absent; two metatarsal tubercles elongate and approximately of the same size, the outer one more salient; interdigital membrane near the toe tips, but on the fourth only a little more than half its length and prolonged as a cutaneous fringe; subarticular tubercles on toes, small and simple. Dorsum light brown with three large darker triangular spots not well marked; one interocular with base to the front and two others on the body with the base to the rear; a vertebral light line divided the last two triangles. Limbs dorsally with transverse wide dark bands. Belly yellowish with dark spots shaped very irregularly.

Dimensions. Head and body 50 mm. Head length 12 mm. Head width 17 mm. Head height 7 mm. Eye 5 mm. Upper eyelid width 4.5 mm. Interorbital space 5 mm. Paratoid length 7.5 mm. Elbow to the third finger 22 mm. Femur 20 mm. Tibia 17 mm. Heel to the fourth toe 28 mm. Foot 20 mm.

Paratypes. CM 4223, 4224, 4226, Incachaca, Dept. Cochabamba, Bolivia. Head and body: 62 mm., 41.5 mm., 37 mm., respectively.

Diagnostic features. Four other species related to *Bufo quechua* have been previously described: *B. ockendeni* Boulenger, *B. inca* Stejneger, *B. leptoscelis* Boulenger and *B. fissipes* Boulenger. In the table below their differential characters and the altitude at which they are found are shown.

	B. ockendeni	*B. inca*	*B. leptoscelis*	*B. fissipes*	*B. quechua*
Cephalic crests	Supraorbitals and parietals	Supraorbitals and parietals	Parietals	Absent	Parietals
Tympanum	Not visible	Visible	Visible	Not visible	Not visible
Paratoids	Subtriangular	Elongate	Subtriangular	Elongate	Elongate
Tarsal fold	One row of granules	One row of granules	Absent	Absent	Absent
Interdigital membrane on fourth toe	Half toe length	Less than half toe length	Half toe length	Very much less than half toe length, rudimentary	More than half toe length
Lateral granules	Each with one point	Each with one point	Crowded and spinose	—	Each with many points
Ventral granules	Rounded	Conical	—	—	Conical
Altitude	1350-1900 metres	1500-1800 metres	1950 metres	1800 metres	2200-2600 metres

From this comparison of characters it may be deduced that *Bufo fissipes*, described from Santo Domingo, Province of Carabaya, Perú, is the nearest relative of *B. quechua*. But *B. fissipes* differs in the absence of parietal crests and the rudimentary interdigital membrane. Comparing the altitudes of the five species, it is noticed that *B. quechua* is seen to live at the highest altitudes; in some localities, such as Yungas de Chapare, Department of Cochabamba, Bolivia, it coincides with *B. ockendeni* but this last lives also at lower altitudes. It is interesting to see that *B. ockendeni* is, in this group of five species, the one that lives at the lowest altitude and has the widest known distribution, from Central and S.E. Perú to the departments of Cochabamba and Santa Cruz in Bolivia. The other three previously described species are restricted to S.E. Perú: *B. inca* (departments of Ayacucho and Cusco), *B. leptoscelis* and *B. fissipes* (Department of Puno, but at different altitudes). *B. quechua* occurs in the Yungas of the Department of Cochabamba, Bolivia.

Material studied (including comparative material). *Bufo quechua:* CM 4223-26 (4 specimens) Incachaca, Department of Cochabama, Bolivia, 2500 m., J. Steinbach.

USNM 118704 (1 specimen) Socotal, Yungas del Chapare, Department of Cochabamba, Bolivia, J. Steinbach, II-1929.

MZUM 89414 (1 specimen) Yungas del Chapare, Department of Cochabamba, Bolivia.

MZUM 76075 (1 specimen) Yungas de Cochabamba, 2200 m., Department of Cochabamba, Bolivia.

MZUM 68163 (3 specimens) Yungas de Cochabamba, 2200 m., Department of Cochabamba, Bolivia.

MZUM 68166 (1 specimen) Cochabamba Valley, 2600 m., Department of Cochabamba, Bolivia.

Bufo fissipes. AMNH 6105 (1 specimen) Juliaca, Perú, H. H. Keays. Chicago Natural History Museum 64879, 64850 (2 specimens) Puno, Perú.

Bufo inca. USNM 107648 (1 specimen) 1 mile above San Miguel, Avacucho, Perú, O. F. Cook, V-27-1915.

MCZ 4758 (1 specimen) Idma, Urubamba Valley, 6000 ft., Perú, E. Heller, X-1915.

Bufo ockendeni. MCZ 15425 (1 specimen) Chaquimayo, Perú. Chicago Natural History Museum 3581-82 (2 specimens) Chaquimayo, S.E. Perú, H. C. Watkins.

AMNH 6111-17 (16 specimens) Juliaca, Perú, H. H. Keays.
MZUM 68153 (1 specimen) Yungas del Chapare, Department of Cochabamba, Bolivia.
MZUM 68152 (2 specimens) Tarata, 1900 m., Bolivia.
CM 3806b, 4515 (2 specimens) Cerro Hosano, west of Santa Cruz, 1400 m., J. Steinbach.

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Plate 1. *Bufo manicorensis*, new species. Type: BMNH 1898.3.10.1.

Plate 2. Left. *Bufo spinulosus spinulosus.* Right. *Bufo spinulosus alti-peruvianus,* new subspecies. Type: AMNH 14418.

Plate 3. *Bufo quechua*, new species. Type: CM 4225.

B R E V I O R A

Museum of Comparative Zoology

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AUSTRALIAN CARABID BEETLES VI. THE TROPICAL AND SOME SUBTROPICAL SPECIES OF *PAMBORUS*, *MYSTROPOMUS*, AND *NURUS*

BY P. J. DARLINGTON, JR.

This is the first of four papers describing new flightless tropical (and a few related subtropical) Australian rain forest Carabidae of zoogeographic importance. However, these special papers will be treated as parts VI to IX of my general series on Australian carabid beetles. Some of the species now described have been referred to (but not by name) in the preceding paper of the series, on transition of wet forest carabid faunas from New Guinea to Tasmania (1961b). My localities are listed, mapped, and briefly described in No. IV of this series (1961a). The holotypes of new species described from my material are placed, at least temporarily, in the Museum of Comparative Zoology. Paratypes will be deposited with the Commonwealth Scientific and Industrial Research Organization at Canberra (where they can be compared with the Sloane Collection) and in most cases in the Queensland Museum too. In the descriptions, proportions are usually given as simple fractions (⅔, ¾, etc.) but are based on actual measurements made under the microscope.

PAMBORUS

Bänninger (1940) has correctly distinguished the real species of *Pamborus* known to him, after examining some of the older types that Sloane (1904) was unable to see. What I have to say now is mostly concerned with tropical forms unknown to Bänninger.

Three species-groups of *Pamborus* occur in tropical North Queensland. Two of them consist of single, very distinct species, *elegans* Sl. and *punctatus* n. sp., respectively. The third, which

I call the *tropicus* group, consists of a series of slightly differentiated, allopatric forms extending from South Queensland to the base of the Cape York peninsula and probably derived from a common ancestor that dispersed rather recently. Characters given in the following key to distinguish the four species (? or subspecies) of the *tropicus* group should be supplemented by comparison of descriptions and of specimens if possible.

Key to tropical species of PAMBORUS (*with some subtropical species in parentheses*)

1. Each elytron with 6 to 8 costae (which may be raised or nearly flat) separated by narrower crenulate intervals 2
— Elytron with 15 or more nearly equal costae 7
2. Tip of aedeagus dentate near apex; neck constriction deep; prothorax subcordate (wet forests of New South Wales and South Queensland) ..... (*alternans*)
— Tip of aedeagus not dentate; neck constriction shallow; prothorax variable in shape 3
3. Form more convex; sides of prothorax not or slightly sinuate; 7th and 8th elytral costae usually strongly developed and not much interrupted (drier woodlands of New South Wales and South Queensland) ..... (*viridis*)
— Less convex; sides of prothorax often more sinuate (*tropicus* group) 4
4. Elytra with costae relatively wide and weakly convex, 5th and 6th nearly as wide as 4th on disc, 7th and 8th usually distinct, but variable 5
— Elytra with costae usually narrower and more convex, 7th and 8th more often interrupted or disintegrated 6
5. Intervals between costae slightly wider and more strongly crenulate; larger (31-36 mm.) (South Queensland) ..... (*subtropicus*)
— Intervals between costae narrower (1st reduced to a fine irregular impressed line) and less strongly crenulate; smaller (26-30 mm.) (Eungella Range) ..... *transitus*
6. Shining (Mt. Spec to Atherton Tableland, etc.) ..... *tropicus*
— Duller (northern Atherton Tableland to Mossman-Daintree area) ..... *opacus*
7. Pronotum with basal impressions, not punctate; elytral costae not much interrupted; elytral margins green (Herberton — ? to v. Cooktown) ..... *elegans*
— Pronotum without basal impressions, entire surface densely coarsely punctate; all elytral costae much interrupted; bluish black (Atherton Tableland, etc.) ..... *punctatus*

Pamborus subtropicus n. sp.

Form of *alternans* but often broader, somewhat variable, slightly depressed; rather shining black, pronotum with marginal channels (narrowly) and posterior impressions bluish or greenish, elytra with crenulate intervals and margins green. *Head*: neck constriction weak. *Prothorax* about ⅓ (Mt. Jacob) or ⅙ (Kenilworth) wider than long at middle; base slightly wider than apex; sides broadly rounded anteriorly, broadly but not strongly sinuate posteriorly; posterior angle moderately produced backward; linear basal impressions uniting with marginal channels in moderate impressions, with convex areas not or vaguely reaching posterior margin; each lateral margin with 1, 2, or 3 (number variable, sometimes asymmetrical) seta-bearing punctures near and before middle. *Elytra* with margins not serrate; each with 8 slightly elevated costae wide on disc, narrower externally and apically, separated by strongly crenulate intervals of which the 1st is narrowest but plainly crenulate; 7th and 8th costae usually distinct at least to near middle of length but not strongly raised, slightly interrupted, 8th sometimes disintegrated. Aedeagus not dentate. Length 31-33 (36); width 12 (13) mm. (figures in parentheses show probable size of an individual of which I have only elytra).

Holotype ♂ (M. C. Z. Type No. 30,346) and 1 ♀ paratype from Mt. Jacob, *c.* 45 miles south of Gladstone, South Queensland, March 1958; and 1 ♂ paratype from Kenilworth, west of Blackall Range, South Queensland, May 1958; all taken by myself in or on the borders of rain forest. I have also elytra of this species from Mapleton, on the north end of the Blackall Range.

See key for distinguishing characters of this species.

Pamborus transitus n. sp.

Form almost of rather broad *alternans*, slightly depressed; moderately shining black, marginal channels and basal impressions of pronotum without or with only slight metallic color, margins and crenulate intervals of elytra green or greenish. *Head*: neck constriction weak. *Prothorax* between ⅙ and ¼ wider than long at middle; base slightly wider than apex; sides broadly rounded anteriorly, sometimes vaguely angulate at middle, broadly but weakly sinuate posteriorly; posterior angles

moderately produced backward; linear basal impressions uniting with marginal channels in moderate impressions, with convex areas sometimes reaching or nearly reaching posterior margins; each lateral margin with 1 to 4 (number variable, often asymmetrical) seta-bearing punctures near and before middle. *Elytra* with margins not serrate; each elytron with 8 slightly elevated costae very wide on disc, narrower laterally and apically, 5th and 6th not or not much narrower than 4th on disc, 7th and 8th narrower, usually distinct but not strong, often somewhat interrupted but rarely disintegrated; crenulate intervals very narrow on disc, less strongly crenulate than in related forms, interval between 1st and 2nd costae reduced to a fine line almost without crenulations anteriorly. Aedeagus not dentate. Length 26-30; width *c.* 10.5-11.5 mm.

Holotype ♂ (M. C. Z. Type No. 30,347) and 67 paratypes all from the Eungella Range, *c.* 40 miles west of Mackay, Queensland, *c.* 2000-3000 ft. altitude, Nov. 1957, taken by my wife, my son, and myself, in rain forest.

For characters and relationships of this geographically isolated form, see preceding discussion and key.

Pamborus tropicus n. sp.

Form almost of *alternans*, slightly depressed; rather shining black, marginal channels and posterior impressions of pronotum and margins and crenulate intervals of elytra green. *Head*: neck constriction weak. *Prothorax* appearing as long as wide but by measurement nearly ⅕ wider than long at middle; base not or slightly wider than apex; sides broadly rounded anteriorly, sometimes vaguely angulate at middle, broadly sinuate posteriorly; posterior angles projecting backward as usual in group; basal impressions uniting with marginal channels in moderate impressions, sometimes with vague convex areas reaching or nearly reaching base; each lateral margin with 1 to 4 seta-bearing punctures near and before middle (number variable, often asymmetrical). *Elytra* with margins not serrate; each elytron with 8 costae usually slightly narrower and more convex than in preceding forms especially externally, but 7th and 8th costae variable, sometimes distinct (but not strong), sometimes much interrupted or disintegrated; crenulate intervals narrow on disc, broader externally, strongly crenulate. Aedeagus not dentate. Length (types) 28-31; width 10.5-11.5 mm.

Holotype ♂ (M. C. Z. Type No. 30,348) and 30 paratypes all from Mt. Spec plateau (Paluma Range), about 40 miles north of Townsville, 2000-3000 ft. altitude, Nov.-Dec. 1957, taken by the Darlingtons, in or on the edges of rain forest. Additional specimens, not types: 5, Kirrama Range, 2000-3000 ft., Dec. 1957; 3, Millaa Millaa, April 1932; 2, Longlands Gap, Sept. 1952 (J. G. Brooks); 6, mountains above (SW of) Atherton, Dec. 1957 and Feb. 1958 (this and the 2 preceding localities are on the south-central Atherton Tableland); 6, Mt. Bartle Frere, west slope, 2000-3500 and 3000-5000 ft., Dec. 1957; and 1, Davies Creek Road, northern Atherton Tableland, May 1958; all specimens except Brooks' collected by the Darlingtons, in rain forest.

This species (or subspecies) is more like *subtropicus* of South Queensland than like *transitus* of the Eungella Range. It differs from *subtropicus* in having elytral costae usually slightly narrower and more convex especially externally, with 7th and 8th costae more often interrupted or disintegrated.

Pamborus opacus Gehin

Sloane (1904, p. 702) and Bänninger (1940) have applied the name *opacus* to this species. It differs from *tropicus* in being obviously duller, and it is also slightly more slender, with slightly narrower and more convex elytral costae, and on the average it has more marginal pronotal punctures, although these vary in number and position.

Although this species and *tropicus* are not very different structurally, I think they probably are real species, for they overlap geographically. Of *opacus*, I have 6 specimens from mountains north of Kairi, on the Atherton Tableland between the Atherton area and Davies Creek, taken in rain forest at close to 4000 ft. altitude, and 18 specimens from Mt. Lewis, near Mossman, taken at about 3000 ft. altitude in rain forest. My northernmost locality for *tropicus* is between these two places but at a somewhat lower altitude, near the southern end of the Davies Creek forestry road.

Pamborus elegans Sloane

Sloane (1915) described this species from "scrub" (rain forest) east of Herberton on the Atherton Tableland. It should occur in the rain forests on the mountains between Atherton and Herberton, but I did not find it. Bänninger (1940) records

it from "Mac Ivor River," which may be the McIvor River north of Cooktown.

Pamborus punctatus n. sp.

Form as figured (Fig. 1); entirely dull bluish or purplish black. *Head* quadrate; eyes small; antennae short; neck constriction very deep. *Prothorax* ⅓ or more wider than long at middle, widest behind middle, narrowed in front and behind

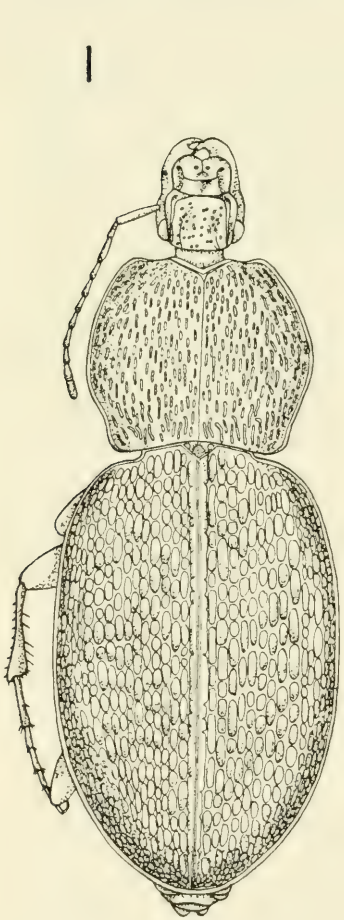

Fig. 1.
Pamborus punctatus n. sp.

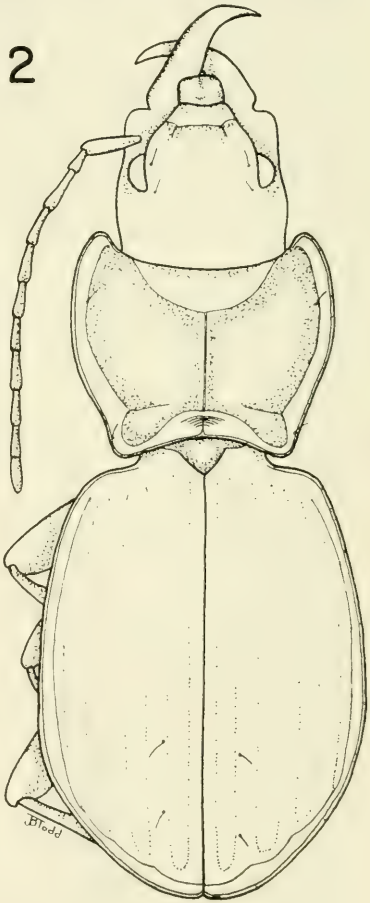

Fig. 2.
Nurus rex n. sp.

but base about ⅓ wider than apex; sides weakly rounded except strongly rounded or vaguely angulate behind middle, slightly sinuate near base; basal angles only slightly produced backward; side margins thickened but marginal channels and basal impressions obsolete; dorsal surface almost evenly but not strongly convex, with middle line almost obsolete except anteriorly, and transverse impressions obsolete; whole surface coarsely, irregularly punctate with longitudinal, deep punctures. *Elytra* oval; humeri not serrate; each elytron with 15 distinct and 2 additional partial costae, all much interrupted, the outermost reduced to tubercles. Abdomen extensively but not uniformly punctate. Tip of last ventral segment subtruncate in male, broadly rounded in female. Aedeagus not dentate. Length 17-19.5; width 7.3-8.0 mm.

Holotype ♀ (M. C. Z. Type No. 30,349) and 2 paratypes from mountains above (SW of) Atherton, 3000-4000 ft. altitude, Dec. 1957 and Feb. 1958; and additional paratypes as follows: 1, south of Ravenshoe, *c.* 3000 ft., Feb. 1958; 2, east side Mt. Bellenden Ker, 3000-4500 ft., Dec. 1957. All specimens taken by myself in rain forest.

This species differs from all previously known *Pamborus* in obliteration of all pronotal impressions and in heavy punctation of pronotum. The small size and numerous elytral costae suggest a distant relationship with *P. guerini* Gory of South Queensland etc., but (in addition to the other differences) *guerini* has serrate humeri and *punctatus* has not.

In life this small *Pamborus* strikingly resembles the heavily catenulate species of *Notonomus* (especially *masculinus* Darl. 1953) which occur in the same rain forest areas. I suspect this is a case of mimetic convergence.

Mystropomus

Two species of this genus occur in tropical eastern Australia. One, with alternate elytral intervals raised, occurs in rain forest on the Eungella Range. It seems to be at most a poorly defined subspecies of *subcostatus* Chd. of South Queensland and New South Wales. I do not think it is worth naming. The other tropical species, with elytral intervals equal, is *N. regularis* Bänninger (1940), which occurs probably throughout the main (base-of-peninsular) rain forest system of North Queensland. I now have 113 specimens of it from localities north to

Thornton Peak and south to the Mt. Spec plateau. There is some geographical variation, but specimens from most localities can be referred to the typical subspecies. However, the form on the Mt. Spec plateau at the southern extreme of the species' range seems worth distinguishing as follows.

Mystropomus regularis laevis n. subsp.

Similar to large specimens of typical *Mystropomus regularis* Bänn. but almost lacking the weak granular elytral costae of typical *regularis*. In the latter each elytron has 6 or 7 distinguishable (though scarcely elevated) costae or stripes that are more shining than the intervening spaces. In the new subspecies only about the 4 inner stripes are indicated at all, and they are much less distinct than in the typical *regularis*. The rest of the elytral surface, including the lateral and anterior declivities, is virtually undifferentiated, dull, and finely granular. As compared with typical *regularis, laevis* also has slightly wider and more reflexed prothoracic margins and a somewhat duller pronotum. Length *c.* 17; width *c.* 6.5 mm.

Holotype ♂ (M. C. Z. Type No. 30,350) and 1 ♂ paratype both from Mt. Spec plateau (Paluma Range), *c.* 40 miles north of Townsville, North Queensland, 2000-3000 ft. altitude, Feb. 1958, taken by myself in or on the edge of rain forest.

Nurus

This is a group of very large, stout Pterostichini that I cannot separate from *Trichosternus* by any single constant character except the relatively heavy build. *Nurus atlas* Cast. has each ♂ front tarsus slightly dilated, with only 2 segments squamulose, and most other *Nurus* have ♂ tarsi narrow and without squamae, but both these conditions exist in certain *Trichosternus*. Tschitschérine (1902) was therefore wrong in using form of ♂ tarsi as a primary generic character and Sloane (1894) was right in not using it. The known species of *Nurus* form several groups that have been called subgenera and that are named in the following key, although I am doubtful of the value of these subgenera.

Nurus sensu stricto includes about 4 species in northern New South Wales, south at least to near Ebor, and an additional

species on Mt. Tamborine in southeastern Queensland.[1] The majority of the species inhabit rain forest, but at least one extends into savannah woodland. The two species of *Pachymelas* apparently inhabit savannah woodland and perhaps coastal habitats in tropical Queensland; they do not seem to enter rain forest. The two previously described species of *Nuridius* are localized in South Queensland, probably in rain forest, although their habitats are not specified. The three new species described below, one tentatively associated with *Nuridius* and the others not assigned to subgenera, are all rain forest species, but they are not directly related among themselves and probably represent three separate invasions of isolated rain forests by different stocks of *Nurus*. The genus is apparently absent in the main (base-of-peninsular) rain forests of North Queensland.

Key to subgenera and some species of NURUS

1. Mesosternum not setose (*Nurus sensu stricto*) ..... *c. 5 species*
— Mesosternum setose anteriorly 2
2. Humeri without teeth (*Pachymelas*) ..... *2 species*
— Humeri with margin toothed or thickened (but sometimes only slightly so) 3
3. Elytra without basal margin (*Nuridius*) 4
— Elytra with basal margin 5
4. Margins of pronotum less strongly reflexed; size smaller (31 & 39 mm.) ..... *fortis, grandis*
— Margins of pronotum strongly reflexed, size larger (41-45 mm.) ...*rex*
5. Wholly black; stout, prothorax transverse, not much narrowed behind ..... *nox*
— Greenish black; more slender, prothorax more narrowed behind ..... *medius*

NURUS REX n. sp.

Form as figured (Fig. 2); large; black, head and pronotum shining, elytra (except marginal intervals) dull, lower surface moderately shining. *Head* rather small (in genus), *c.* 2/3 width prothorax; mandibles long, straight basally, strongly

[1] The type locality of *N. imperialis* (Sloane 1894) is given as "North Queensland," but the species really inhabits South Queensland. I have seen it only from Mt. Tamborine south of Brisbane. The type locality of *N. crassiformis* (Sloane 1899, p. 570) is given as "Cairns," but the specimen was received from French, and I know from other evidence that many of French's specimens have wrong localities. If *crassiformis* is a synonym of *atlas*, as supposed, the type presumably really came from northern New South Wales.

curved before apex, with irregular row of small seta-bearing punctures near lower edge of outer face near base; antennae short, extending only slightly beyond basal angles of prothorax; eyes small, genae long, wider than eyes, slightly, sinuously narrowed to neck; 2 supra-ocular setae each side; frontal impressions subparallel, irregular; mentum with deeply emarginate tooth. *Prothorax* cordate, 3/5 or slightly less wider than long at middle, strongly narrowed behind, less so in front; base slightly narrower than apex; latter broadly emarginate, with anterior angles abruptly advanced; base emarginate, posterior angles produced backward in arc of emargination; sides rounded anteriorly broadly but usually not strongly sinuate well before base; basal angles would be right or slightly acute except narrowly rounded; lateral margins wide, very wide posteriorly, strongly reflexed, each with 1 or 2 seta-bearing punctures before middle and 1 or 2 also near base; base margined, apex not; disc with well impressed median line and transverse impressions; posterior impression and marginal channels joining in obliquely flattened baso-lateral areas; surface of disc slightly transversely wrinkled but not punctate, except extreme base at middle rugose-punctate with elongate punctures. *Elytra* broad, widest behind middle; humeri obtuse, with margins forming teeth which are strongly raised but hardly prominent laterally; base not margined (margins ending inwardly about opposite ends 5th striae); disc very convex; each elytron with 7 finely punctate striae lying in broad depressions between slightly elevated intervals; 9th interval with row of minute foveae (the 8th stria) along inner edge; no 10th interval; 7th interval scarcely raised at base; each 3rd interval 2-punctate posteriorly, usually near top of and well down on declivity, but position of punctures variable. Lower surface: prosternal process and anterior face of mesosternum setose; ventral segments 2 to 5 with some irregular setigerous punctation. Male tarsi not dilated, without squamae; ♂ usually with 1, ♀ 2 principal setae each side last ventral segment, but additional, usually smaller setae sometimes present. Length 41-45, width 15-17 mm.

Holotype ♂ (M. C. Z. Type No. 30,351) and 12 paratypes all from the Elliot Range, south of Townsville, Queensland, taken at about 3000 ft. altitude, March 2, 1958, by my son and myself, under logs in mountain rain forest.

See preceding discussion and key for place of this species among other *Nurus*.

NURUS NOX n. sp.

Large; black, moderately shining above and below except elytra duller with narrow bands along 8th striae (sometimes including margins) more shining. *Head* of moderate size (in genus), ¾ or slightly less width prothorax; mandibles rather long, strongly curved before apex, without setigerous punctures on lower outer face near base; antennae extending beyond base of prothorax by two or more segments; eyes small; genae subparallel, slightly sinuate but not much narrowed to neck; 2 supra-ocular setae each side; frontal impressions weak, subparallel, irregular; mentum with emarginate tooth. *Prothorax* transverse-subquadrate, slightly more than ½ wider than long at middle, weakly narrowed behind; base about 1/10 wider than apex; latter slightly emarginate, with anterior angles only slightly advanced; base broadly emarginate at middle, subtruncate at sides; base and apex unmargined; sides arcuate anteriorly, then nearly straight and slightly converging posteriorly for much of length, then broadly and usually rather slightly sinuate before base; basal angles *c.* right but narrowly rounded; lateral margin moderate, slightly wider posteriorly, moderately reflexed, each with seta-bearing puncture near or a little before base but without anterior-marginal setae; disc with usual middle line and deeper transverse impressions; basal impression and marginal channels joining in what would be large baso-lateral impressions except each impression occupied by a large convex space; surface of disc slightly transversely wrinkled but not punctate, wrinkling much closer at sides and base, radiating from a central point near base. *Elytra* wide, not much narrowed anteriorly; humeri rounded, minutely obtusely toothed or at least slightly thickened at humeri (teeth or thickenings easily overlooked in dirty specimens); base margined almost to scutellum; disc very convex; each elytron with 7 vaguely indicated, sometimes finely punctate striae in depressions between slightly convex intervals; 9th interval (marginal channel) with an irregular series of small ocellate foveae on inner edge (= 8th stria); no 10th interval; 7th interval only slightly raised at base; each 3rd interval usually 2-punctate with punctures near top of and well down on declivity, but punctures variable in position and sometimes missing. Lower surface: prosternal process and anterior face of mesosternum setose; ventral segments 2 to 5 with setigerous punctures tending to form transverse rows. Male with front

tarsi not dilated, without squamae; male with 1 or 2, female with 2 or more principal setae each side last ventral segment, but setae variable, not always distinguishing sexes. Length 30-37; width 11.5-15 mm.

Holotype ♂ (M. C. Z. Type No. 30,352) and 7 paratypes (5 whole specimens and 2 represented by shells of prothorax and elytra) all from Mount Jacob, about 45 miles south of Gladstone, South Queensland, *c.* 2000 ft. altitude, March 1958, taken by the Darlingtons in and on the edges of rain forest.

This new species approaches *Pachymelas,* for the humeral "teeth" are small, obtuse, and inconspicuous, sometimes only slight thickenings of the margin, but the present species differs from the two known *Pachymelas* (both of which are before me) in a number of specific characters, including form of prothorax and presence of shining *sub*marginal stripes on elytra.

Nurus medius n. sp.

Rather slender (in genus); greenish or bluish black, shining above except elytra duller with more or less shining sutural intervals and marginal channels, rather dull greenish below. *Head* large, 4/5 or slightly less width prothorax, mandibles rather long, curved before apex, without setigerous punctures on lower edge of outer face; antennae relatively long, passing basal angles of prothorax by about 3 segments; eyes small, genae wider than eyes, broadly rounded, slightly narrowed to neck; frontal impressions weak, subparallel; mentum with emarginate tooth. *Prothorax* subcordate, between 1/3 and 1/2 wider than long at middle; sides weakly rounded anteriorly, straight and converging posteriorly behind middle, then broadly sinuate before right or slightly acute, scarcely blunted posterior angles; base about equal to or slightly narrower than apex; latter broadly emarginate at middle, slightly rounded at sides, with anterior angles (marginal channels) slightly advanced; base broadly emarginate, subtruncate at sides; base and apex unmargined; lateral margins rather narrow (in genus) and not strongly reflexed, sometimes slightly scalloped, each with one seta before middle and another almost on posterior angle; disc with usual middle line, moderate anterior transverse impression, and deeper posterior transverse impression; latter ending in rather vague, irregular baso-lateral depressions which include somewhat transverse convexities near base; surface of disc slightly wrinkled, more wrinkled at base, the basal wrinkles

radiating irregularly from central point. *Elytra* rather strongly narrowed anteriorly, with obtuse humeri; latter with small but distinct teeth; basal margins entire; each elytron with 7 fine, faintly punctate striae in depressions between low, rounded intervals; 7th interval elevated at base but not acute; 3rd interval 2- or 3-punctate posteriorly, above and on declivity. Lower surface: prosternal process setose; mesosternum rather sparsely setose in fresh specimens, but seta sometimes hard to detect in old ones; ventral segments 2 to 5 with a few (variable) setigerous punctures tending to form transverse rows near middle of segments posteriorly. Male with front tarsi not dilated and without squamae; ♂ with 1, ♀ 2 setae each side last ventral segment. Length 30-37; width *c.* 11.5-14 mm.

Holotype ♂ (M. C. Z. Type No. 30,353) and 26 paratypes all from the Eungella Range, west of Mackay, Queensland, 2000-3000 ft. altitude, Nov. 1957, taken by the Darlingtons in rain forest.

This new species resmbles *Nurus sensu stricto* in form and metallic coloration but differs in presence of setae on the mesosternum.

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BREVIORA

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MIOCENE LIZARDS FROM COLOMBIA, SOUTH AMERICA

BY RICHARD ESTES[1]

Numerous fossil vertebrates were collected by the 1949 University of California field expedition to the upper Magdalena Valley, Huila, Colombia, South America. Among these, the lower vertebrates include bony fishes, lepidosirenid lungfish, a bufonid frog (identified as ?Leptodactylidae by Savage, 1951), turtles, crocodiles, snakes, and lizards. The lizards are described in the present paper.

I am indebted to Dr. Wann Langston for bringing these specimens to my attention, and to Mr. C. M. Bogert, American Museum of Natural History, Dr. Ernest E. Williams, Museum of Comparative Zoology, Harvard University, and to Dr. Alan Leviton, California Academy of Sciences, for the use of comparative material in their collections.

The manuscript has been read by Drs. J. T. Gregory and D. E. Savage, University of California, Museum of Paleontology, and Dr. Ernest E. Williams, and I wish to thank them for numerous helpful suggestions.

The sequence and distribution of the fossil faunas of the Magdalena Valley has been discussed by Stirton (1953, see especially figures 1, 2). Fossil lizards have been found only in the Upper Oligocene Coyaima fauna, and the Upper Miocene La Venta fauna.

Abbreviations. A.M., American Museum of Natural History, Department of Vertebrate Paleontology. U.C., University of California, Museum of Paleontology.

[1] Department of Biology, Boston University, and Research Associate, Department of Vertebrate Paleontology, Museum of Comparative Zoology, Harvard University.

COYAIMA FAUNA
Family TEIIDAE
cf. Tupinambis sp.

Referred specimen. U. C. no. 56303, maxillary fragment.

Locality. U. C. loc. V-4411, Coyaima, Colombia, South America.

Age. Late Oligocene.

Description. The fragment is the posterior end of a right maxilla, which bears one complete tooth and the bases of three others. The complete tooth has a strongly wrinkled crown surface, and in occlusal view is circular. No anteroposterior crests are present.

Discussion. The tooth closely resembles posterior maxillary teeth of Recent *Tupinambis teguixin*. It differs from comparable teeth of *Dracaena* in not being dorsoventrally flattened.

LA VENTA FAUNA
Family TEIIDAE
Tupinambis cf. T. teguixin

Referred specimen. U. C. no. 38856, left dentary and splenial, with parts of the coronoid, angular and surangular; the symphysis region missing. Collected by Dr. José Royo y Gomez.

Locality. U. C. loc. V-4526, Lower Red Beds, Honda group, Huila, Colombia, South America.

Age. Late Miocene.

Description. The maximum length of the specimen is forty-three millimeters. The dentary is robust, and has a heavy shelf external to the tooth row. Three inferior alveolar foramina are preserved. Posteriorly a large re-entrant notch contains a fragment of surangular. The latter, and part of the dentary anterior to it, is prominently depressed for muscle insertion. The splenial is large, and deep anteriorly as in most teiids. There are two foramina in the splenial, the posterior one smaller. The anterior process of the angular inserts between the splenial and dentary, and reaches only as far forward as the level of the penultimate tooth. The coronoid is represented only by the interior dentary process, which is inserted into a notch between splenial and dentary. The teeth are bulbous and have slightly crenulated surfaces. Immediately posterior to the broken anterior end of the specimen a pit is present for a replacement

tooth. The subsequent teeth (referred to here by numbers 1-8) form a slightly curved series when viewed dorsally, and the line of occlusion viewed laterally has a slight dorsoposterior curve. Tooth one is slightly bulbous and smaller than tooth two.

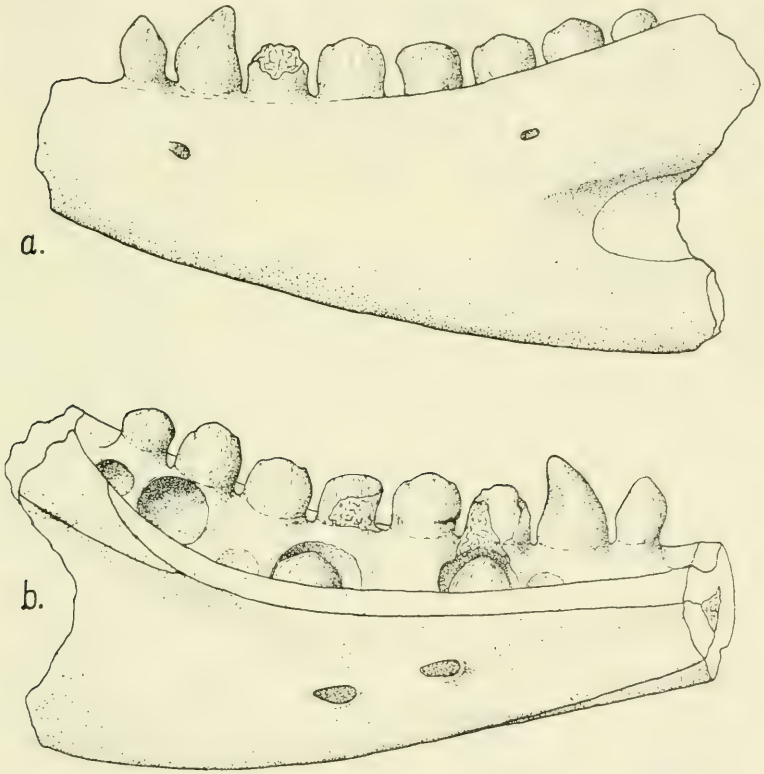

Figure 1. a. *Tupinambis* cf. *T. teguixin*, U. C. no. 38856, labial view of left dentary, x 2. b. The same, lingual view.

Two is taller and slimmer than the succeeding teeth and is slightly recurved and concave posteriorly. Tooth three is being replaced, its crown is broken, and its thin eroded base has been crushed ventrally so that the tooth appears lower than it actually was; measurement of the replacement tooth indicates that it would be intermediate in height between the preceding and succeeding teeth. The replacement pits under the first and second teeth are in the interdental position. Teeth four and five are subequal; four has a faint anterior and posterior crest near

the crown. The crown of tooth five is worn smooth. The large, fully formed replacement tooth below it has a slightly crenulated surface near its apex, and its anteroposterior crests are connected to the central point of the crown. Teeth six and seven are subequal and slightly smaller than teeth four and five, and the crests on tooth six are slightly worn on the occlusal surface. Tooth seven is worn smooth and is being replaced, but the replacement tooth is missing. Tooth eight is about one-half the size of the rest of the teeth, has anteroposterior crests, and a large replacement crypt below it. All of the teeth are essentially round, but the last few show a slight tendency to be longer than wide.

Discussion. The jaw is about the same size as that of the *Dracaena* described below, and very slightly larger than that of the largest *Tupinambis teguixin* seen by me. It differs from *Dracaena* in having teeth which are higher than broad (or only slightly lower than their broadest dimension), and which are not as prominently constricted at the base; in having a depressed area on the surangular region; and in having teeth with anteroposterior crests. The only characters in which the fossil differs from specimens of Recent *T. teguixin* are the concave splenial and the size of the posterior teeth. The splenial is concave in *Dracaena* and in some species of *Cnemidophorus,* but is usually flat or slightly concave to convex in *Tupinambis.* In the fossil, however, the concavity may in part be the result of postmortem shrinkage or crushing and is not conclusive. The posterior teeth of *Tupinambis teguixin* are usually relatively slightly smaller than those of the fossil, and are often more linguolabially compressed, though this character varies. The minor differences between the fossil as preserved and Recent specimens do not seem to warrant taxonomic separation. The other Recent species, *T. nigropunctatus,* has higher crowned, smooth, and prominent cuspate teeth, and is smaller than *T. teguixin.*

Rovereto (1914a) described several fossil species of *Tupinambis* from the Pliocene of Argentina. Their validity is difficult to determine at the present time, but they seem to resemble *T. teguixin* most closely.

Dracaena colombiana n. sp.

Type. U. C. no. 39643, complete right dentary, collected by Dr. R. W. Fields.

Referred specimens. U. C. no. 40277, distal and proximal ends of a left femur, catalogued as float from ?Cerbatana gravels. U. C. no. 37899, sacrum and associated first caudal vertebra, collected by Dr. José Royo y Gomez from U. C. loc. V-4517, Monkey Unit. U. C. no. 38927, posterior half of right maxilla, with bases for three teeth, from U. C. loc. V-4528, Upper Red Beds. The four localities occur within an area about six kilometers in diameter.

Type locality. U. C. loc. V-4536, San Nicolás, near Villavieja, Huila, Colombia, South America. San Nicolás clays, Honda group.

Age. Late Miocene.

Diagnosis. Differs from the Recent *Dracaena guianensis in* the following characters: dentary larger and more robust; tooth row more strongly curved upward posteriorly; tooth outline round or suboval; tooth number fifteen. From the living *D. paraguayensis* it differs in possessing five more dentary teeth. It differs from *Tupinambis teguixin* in having more posteriorly expanded cheek teeth, which are larger, basally constricted, and wider than high, and in lacking a depression in the exterior notch for the surangular.

Description. The dentary is 60 millimeters long. The Meckelian fossa is widely open. The robust symphysis has a rugose

Figure 2. *Dracaena colombiana,* n. sp., U. C. no. 39643, type specimen, Miocene, Colombia, South America. Labial view of right dentary, x 1.5.

articular surface, and is separated from the main body of the dentary by a linguolabial constriction. There are five inferior alveolar foramina, and the dentary is rugose labially near the symphysis, probably for the genioglossus muscle. A broad shelf

is present labial to the tooth row. The labial coronoid notch is prominent, and reaches as far forward as the anterior border of the last tooth. There are fifteen subpleurodont (or subacrodont) teeth, of which all but six are preserved. Teeth one through five are missing; six and seven are conical and slightly striated. The eighth is missing, but the base shows that it was molariform. Teeth nine to fifteen are molariform, and the ninth projects well above the preceding and succeeding teeth. Beyond the ninth, the teeth are flattened, button-like, and have finely striated, round or suboval crowns, which increase in diameter to the twelfth tooth and then decrease posteriorly. Most of the molariform teeth have occlusal attrition facets, especially tooth twelve. Teeth seven through fifteen have replacement pits at their bases, and several of these pits (eight, ten, twelve, fourteen) contain almost full term replacement teeth. The tooth replacement is directly successive, and apparently alternate.

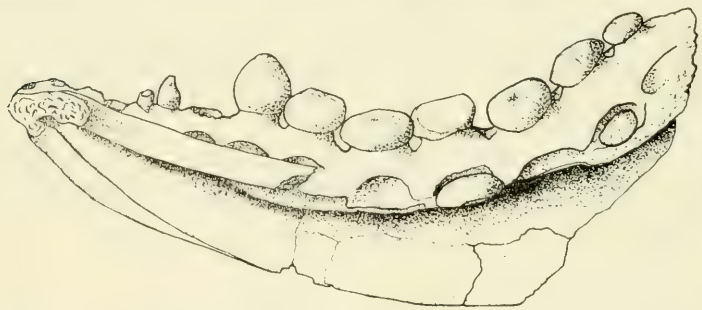

Figure 3. *Dracaena colombiana*, n. sp, U. C. no. 39643, type specimen, Miocene, Colombia, South America. Lingual view of right dentary, x 1.5.

The fragment of maxilla is robust, externally concave, and bears the bases of three large molariform teeth, of which the second has a replacement pit containing a large, flattened replacement tooth.

The femur has been broken, and there is a section of the diaphysis missing. It has been restored to a length of 75 millimeters, by analogy with femora of *Dracaena guianensis*. It is large, but not especially robust, and the patellar groove and muscle attachment scars are prominent. A small U-shaped notch separates the head from the trochanter major.

The sacrum is composed of two co-ossified vertebrae, which have prominent zygosphene-zygantrum articulations. The maximum length of the sacrum from center of cup to tip of ball is

20 millimeters. The greatest width from the centers of iliosacral articulation is 45 millimeters. The first caudal vertebra has a perfectly hemispherical cup and ball, and a prominent zygosphene-zygantrum articulation. It is 16 millimeters long from center of cup to tip of ball.

Discussion. The distinctive specialization of the teeth of *Dracaena* has long been known. Owen (1845) figured a specimen, and Peyer (1929) discussed the form and function of the teeth. Amaral (1950) has described another Recent species, *D. paraguayensis,* but I have not seen a specimen.

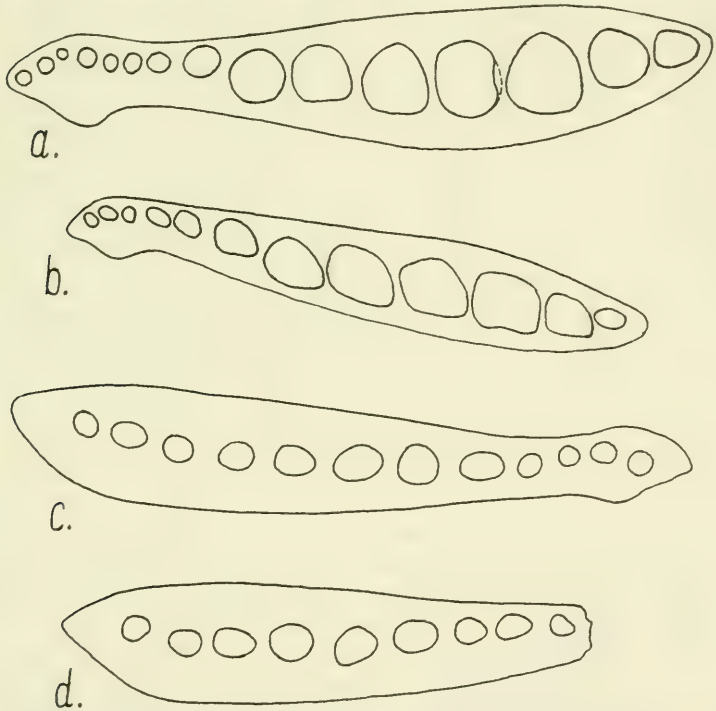

Figure 4. a. Outline of occlusal view of right dentary, *Dracaena colombiana,* U. C. no. 39643, Miocene, Colombia. b. The same, Recent *D. guianensis.* c. The same, left dentary, Recent *Tupinambis teguixin,* A. M. no. 62545. d. The same, *Tupinambis* cf. *T. teguixin,* U. C no. 38856, Miocene, Colombia. a.-d. x 1.5.

The principal differences from the Recent *D. guianensis* are as follows: (1) The fossil is more subpleurodont in tooth implantation, resembling other teiids, whereas the Recent species

tends to be subacrodont. (2) *D. colombiana* has fifteen dentary teeth, *D. paraguayensis* has ten (*fide* Amaral) and *D. guianensis* twelve. (3) The anterior teeth, as far as they are preserved, are less bulbous than in the Recent species. (4) The occlusal outline of the tooth crowns is round or suboval in the fossil and suboval or subrhombic in *D. guianensis*. (5) The crown surface of the molariform teeth is more flattened, and the dorsoventral compression of the entire tooth is less in the fossil.

The referred skeletal elements are somewhat larger than would be expected for a modern *Dracaena* with a dentary the size of *D. colombiana,* as the appendicular skeleton is relatively small in the Recent species. If correctly referred, the skeletal elements perhaps came from a larger individual. The sacrum and first caudal vertebra are characteristically teiid, having a perfectly round cup and ball, and strongly developed zygosphene-zygantrum. They resemble comparable bones of Recent *Dracaena* more than those of Recent *Tupinambis*. The femur has the deep patellar groove seen in many teiids and resembles *Dracaena* in having more separation between head and trochanter major than that seen in *Tupinambis*. The lack of a pronounced fossa posterior to the condyles resembles the condition in *Dracaena*. Some of these bones may be referable to the *Tupinambis* described above, but on the basis of present comparisons, all are referred to *Dracaena colombiana*.

Family IGUANIDAE

Unidentified Genus and Species

A fragmentary left dentary of an iguanid, U. C. no. 39644, from U. C. loc. V-4517, Monkey Unit, shows some similarity to the living *Polychrus*, but lacks the vertical wrinkling of the

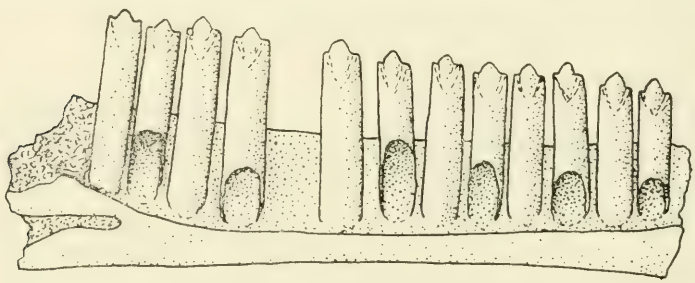

Figure 5. Iguanidae, unidentified genus and species, U. C. no. 39644, Miocene, Colombia, left dentary, broken anteroposteriorly, x 10.

tooth surface found in the latter. Many iguanid genera were compared with this fossil, but close correspondence was not found. It may be new or represent one of the forms not seen, and further identification was thus not attempted.

ECOLOGICAL AND ZOOGEOGRAPHICAL CONSIDERATIONS

Fields (1957, p. 394-395, and 1959, p. 428-429) has described the upper Magdalena Valley area during the late Miocene as a vast floodplain, subject to alternating periods of flooding and drying in a wet-tropical climate. Dry seasons resulted in extensive development of swamps and mudflats, and wet seasons were times of periodic, extensive flooding. The fossil mammalian fauna has a dominantly savannah aspect, but also includes riparian and aquatic types.

Recent *Dracaena guianensis* is particularly abundant in tidal marshy sections and swamps of the Amazon Valley, and Recent *D. paraguayensis* (more primitive in scutellation, yet having a reduced tooth count) inhabits drier ground on the fringes of the swamps in southern Brazil and Paraguay. The fossil *Dracaena colombiana* is found in the Upper Red Beds (playa lake deposit), San Nicolás clays (lacustrine deposit), and the Monkey Unit (sheet floodplain deposit). *Tupinambis* cf. *T. teguixin* occurs in the Lower Red Beds (playa lake deposit). These units all reflect a regional marshy floodplain environment. According to Fields (*op. cit.*) the Magdalena Valley in this region today has a semi-arid climate and is between four and five hundred meters above sea level in the area where these sediments were deposited. Neither *Tupinambis* nor (especially) *Dracaena* usually occur at this altitude, for both are humid-tropical types. They are thus in accord with structural and depositional indications in the sediments (*op. cit.*) for a lower altitude and moister climate in this area during the late Miocene.

These fossils constitute a considerable range extension for the genera involved. *Dracaena* is found today from the Guianas southward to the Amazon, Tocantino, and São Francisco basins, and from the southern Matto Grosso region, Brazil, south to the District of Chaco, Paraguay (Amaral, 1950). *Tupinambis* occurs over much of the forested districts of tropical South America from Trinidad south through the Guianas to Uruguay. Thus, nearly a thousand miles separate the fossils from their nearest Recent representatives. It is apparent that these genera were

once much more widely distributed over northern South America than they are at present, and that their habitat has been restricted both by uplift and by increasing aridity.

The presence of *Tupinambis* in these late Oligocene and late Miocene sediments indicates an early Tertiary origin for this genus, and perhaps also for *Dracaena*. The bufonid frog mentioned in the introduction is closely related to the Recent South American species *Bufo alvarius* and *B. crucifer,* and further heightens the modern aspect of the late Miocene herpetofauna of northern South America. It is clear that modernization of at least part of this fauna took place not later than the Miocene, and quite probably much earlier.

SUMMARY

The teiid lizards *Dracaena colombiana,* n. sp., and *Tupinambis* cf. *T. teguixin,* and an unidentified iguanid lizard occur in the late Miocene La Venta fauna, Colombia, South America. The fossil teiids, found a thousand miles from their nearest modern representatives, indicate a once greater distribution for these genera in northern South America. Their presence corroborates previous interpretation of the La Venta region during the late Miocene as a moist, swampy, lowland floodplain.

A fragmentary specimen from the Coyaima fauna shows the presence of *Tupinambis* sp. in the late Oligocene of the same region.

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BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. AUGUST 21, 1961 NUMBER 144

A LARGE OPHIACODONT PELYCOSAUR FROM THE PENNSYLVANIAN OF THE PITTSBURGH REGION

By ALFRED SHERWOOD ROMER

The presence in the early Permian of a varied series of pelycosaurs indicates that the beginnings of this synapsid group occurred well back in Carboniferous times. Pennsylvanian remains of pelycosaurs are, however, very rare. Because of this paucity of data, the remains described below are worthy of record despite their incomplete and fragmentary nature.

Along the course of McKnight Road, about 6 miles north of Pittsburgh, Pennsylvania, there has recently been considerable quarrying of sand and shale deposits of Conemaugh age in order to level the surface for building construction. The materials quarried were used as fill in North Park, several miles farther north. During the course of this work geology students at the University of Pittsburgh noticed three pieces of bone in freshly dumped park fill; through the courtesy of Mr. Martin Bender of the University's geology department they were deposited in the Carnegie Museum. Inquiry made it rather certain that this material had been excavated from a locality on the east side of McKnight Road near the junction of Brown's Lane. The sandstone excavated here, lies just above the Ames limestone, and hence pertains to the upper part of the Conemaugh group of the Pennsylvanian. It seems certain that all three of the fragments, pertaining to a right shoulder girdle and front leg, were parts of a single, presumably articulated, specimen, but the state of the quarrying operation precluded any attempt to find further remains. The specimens are entered as no. 13942 in the vertebrate paleontology collections of the Carnegie Museum, Pittsburgh; I am indebted to Curator Craig Black for placing them in my hands for description. Needed preparation was done at the Museum of Comparative Zoology under a grant from the National Science Foundation.

The most revealing specimen consists of the distal half of a right humerus. It is clearly pelycosaurian in nature and, it would seem, equally certainly ophiacodontid, the diagnostic features being the greatly expanded entepicondyle, the transversely directed supinator process and the strong development of the lateral margin of the ectepicondyle. In addition, the preserved portion of the shaft indicates that proximal and distal halves of the bone were sharply twisted on one another as in ophiacodonts and in contrast to the lesser torsion in other pelycosaur groups. The overall breadth is 96 mm. The bone is almost exactly superposable on a mature *Ophiacodon* humerus in the M.C.Z. collections (no. 1426) from the Archer City bonebed (Putnam formation). This Texas element is 120 mm. in length, and pertains to a small individual of *O. retroversus* or to an immediate predecessor of that species. If the proportions of the present form were similar to those of *Ophiacodon*, the animal in life would have had a length of head and trunk combined of about 109 cm., and a total length (including the usual long pelycosaurian tail) of about 204 cm. or about 6′8″.

Our Pennsylvanian specimen thus appears to be one of the largest of ophiacodonts, exceeded in size only by *O. retroversus* and *O. major* of the later Wichita formations and by *Stercorhachis dominans* of the European Permian. Post-mortem, the bone has lost the hemispherical ventral swelling with which the radius articulated; the supinator process is imperfectly preserved and there has been some slight damage to the ventral surface at the end of the entepicondyle. Otherwise, apart from crushing, the bone is well preserved. Notable and possibly significant is the fact that ossification had been completed at the time of death. This is in contrast to most specimens of *Ophiacodon*, in which but a small fraction of limb bones show complete ossification of their ends, even when the animal appears to have reached a "mature" size.

Although the general pattern of the bone is comparable to that of *Ophiacodon*, there are definite differences in detail. The present specimen has, dorsally, a prominent muscle scar proximomedially situated near the end of the entepicondyle; this is not present in *Ophiacodon*. The ridge extending proximally along the lateral margin of the ectepicondyle is better developed in the present form than in *Ophiacodon*. The supinator process appears to be less developed than in that genus, but the apparent difference is due to post-mortem damage in our specimen.

A second fragment preserved is the proximal end of the right ulna. This has been greatly crushed, so that the sigmoid articular surface for the humerus is unnaturally narrow, and identification of diagnostic features is difficult. As in the case of the humerus, ossification is practically complete so that, in contrast to most *Ophiacodon* specimens, the whole olecranon is represented by bone rather than cartilage.

A third fragment is the upper end of a right scapula. The posterior margin is thickened and rounded in typical pelycosaur fashion. The lower posterior portion of the piece preserved is somewhat crushed and distorted, but there is an increase in thickness and a curvature of this border such as one would expect as the supraglenoid region is approached. In many pelycosaur specimens, even when seemingly "mature," the upper end of the scapular blade has a thickened distal edge obviously continued in cartilage. The present specimen, which appears to be nearly intact in the posterior part of its upper end, shows no such terminal surface; ossification was apparently complete. More anteriorly the bone has been damaged so that for about 6 cm. there is a thick broken margin on the preserved portion. Beyond and below this the margin as preserved, although imperfect, is thinner where broken off. Probably the missing area here had about the extent indicated by the broken line in the figure. The anterior margin flares out laterally to a marked degree from the general plane of the scapular blade. It seems fairly certain that there was considerable constriction in the width of the blade toward the bottom of the preserved segment. This is in contrast with *Ophiacodon* and *Varanosaurus* in which the scapular blade is broad throughout its height (the scapula of *Clepsydrops* is incompletely preserved).

Fragmentary as are the remains here described, they show definitely the presence at this horizon, fairly well down in the Upper Carboniferous, of a large pelycosaur which is surely an ophiacodontoid and nearly equally surely an ophiacodontid, antecedent although probably not ancestral to *Ophiacodon* of the Permian. Despite its incomplete nature, this fossil deserves taxonomic standing because of its importance in the story of pelycosaur evolution, and it is herewith made the holotype of *Clepysdrops? magnus*, sp. nov. It will not probably prove, when better known, to be generically distinct from *Clepsydrops*, but it appears to be related to that genus, likewise of late Carboniferous age, and it may be provisionally included in it. Because of imperfect knowledge of comparable anatomical features, we may

for the present rely for diagnosis simply on the size, which is approximately half again that of specimens assigned to the genotype, *C. collettii*.

Advantage may be taken of the present opportunity to mention a few fragmentary remains of Pennsylvanian pelycosaurs found in Ohio by Dr. Donald Baird and Mrs. Baird during a 1955 expedition of the Museum of Comparative Zoology. (1) M.C.Z. no. 2411 is from the Summerfield limestone of the Conemaugh group; the locality lies in Center Township, Noble County, Ohio, on the south side of state highway 78, just west of its junction with route 147. Found here were a crushed claw-shaped ungual phalanx 24 mm. long, comparable to the unguals of *Clepsydrops*, two complete pelycosaur centra with transverse diameters of 20 and 14 mm., and a fragmentary centrum with an estimated diameter of about 15 mm. (2) M.C.Z. no. 2295 from the Ewing limestone of the Conemaugh, in the central part of section 7, Noble Township, Noble County, a fragment of a centrum with an estimated diameter of 20 mm. or so. (3) M.C.Z. no. 2777, from the Lower Uniontown limestone of the Monongahela group, along Leith Run Road 3.8 miles from the junction with state route 7, Washington County, Ohio, an ungual phalanx comparable to that mentioned under no. 2411. It may be noted that this is the only identified reptilian bone from the Monongahela. There is, of course, little in these fragments to allow us to give any positive generic determination. But since these specimens are within the size range of the Illinois materials of *Clepsydrops* they may be provisionally referred to that genus.

As mentioned earlier, described pelycosaurian remains from the Carboniferous are very rare indeed. Their rarity is presumably to be correlated with the fact that most Carboniferous fossil localities are from coal swamps in which, apart from amphibious ophiacodonts, pelycosaurs would not be expected. Previously described are: (1) Numerous isolated elements of a small ophiacodontid, *Clepsydrops* (Romer and Price, 1940, pp. 212-216) from the McLeansboro formation near Danville, Illinois. (2) A fragmentary spine of a small *Edaphosaurus* from the Round Knob formation of the Conemaugh group near Pitcairn, Pennsylvania (Case, 1908, pp. 237-238; Romer and Price, 1940, p. 388). (3) From the late Stephanian of Kounova, Bohemia, a single vertebra of a similarly small *Edaphosaurus* (Romer and Price, 1940, p. 388). (4) From the same locality, a number of bones which represent a sphenacodont of good size, to which the name *Macromerion schwarzenbergii* is applicable (Romer, 1945, pp. 429-431).

Little as we know of Pennsylvanian pelycosaurs, a few general conclusions can be reached. That our scanty data on Carboniferous pelycosaurs should include remains of ophiacodonts such as *Clepsydrops* is not surprising. It is believed that the ophiacodontoids are the most primitive of pelycosaur stocks and would hence be expected to appear at an early period in the record. Further, it is believed that many, at least, of the ophiacodontids were amphibious in habit — essentially piscivorous water-dwellers whose ancestors had never abandoned an aquatic existence. In consequence the chances of finding ophiacodonts in the coal swamp deposits which constitute most of the Carboniferous record is much greater than of finding representatives of the more terrestrial sphenacodontoids or edaphosauroids.

Any idea that the finding of *Clepsydrops* in the Conemaugh takes us near in time to the point of origin of the pelycosaurs is an illusion. For fragments of edaphosaur spine have been recovered not only from the very late Kounova deposit but also from the Round Knob formation of the Conemaugh. *Edaphosaurus* is a highly specialized end form. It is obvious that its evolution from an ancestral pelycosaur must have begun at a time much further back in the Carboniferous than the Conemaugh. The assumption (not an unreasonable one) that the major pelycosaur groups evolved independently from a captorhinomorph stock only begs the question.

In general, reptilian stocks of any sort begin with forms that are of small size (as well as of primitive nature) and become increasingly larger as their history progresses. Such a process seems clear in the Lower Permian history of the pelycosaurs. The earliest dimetrodonts of the Texas Wichita were relatively small, and giants developed in the Clear Fork; *Edaphosaurus* species increase greatly in size in later beds; the caseids grew from small forms to enormous *Cotylorhynchus* species; even *Ophiacodon* (which became extinct before the typical Clear Fork) developed from small forms in the lower Wichita and New Mexican beds to the relatively gigantic *O. major*, in the Clyde Formation.

Until the discovery of the present specimen of *C. magnus* the known Pennsylvanian pelycosaur material fell in line with the belief that all early pelycosaurs were small. The *Clepsydrops* specimens from Illinois and Ohio represent small animals, as do both Pennsylvanian scraps of *Edaphosaurus*. To be sure, *Macromerion* of Kounova is a good-sized sphenacodont, but Kounova is close to the Permian boundary and *Macromerion* could be regarded as a slightly premature representative of the Permian

trend to large size. The discovery of *C. magnus*, however, destroys the illusion, for, as noted, this animal was larger than most of his later Permian relatives.

When and if we ever come upon Upper Carboniferous deposits with a representative terrestrial, rather than coal-swamp fauna, it can be confidently predicted that there will be included a considerable number of pelycosaurs which will vary widely in structure and size. It seems certain that for the origin of this fauna, of which so far we have but slight traces, we must look far back in the Carboniferous, to at least early Pottsville or Namurian levels.

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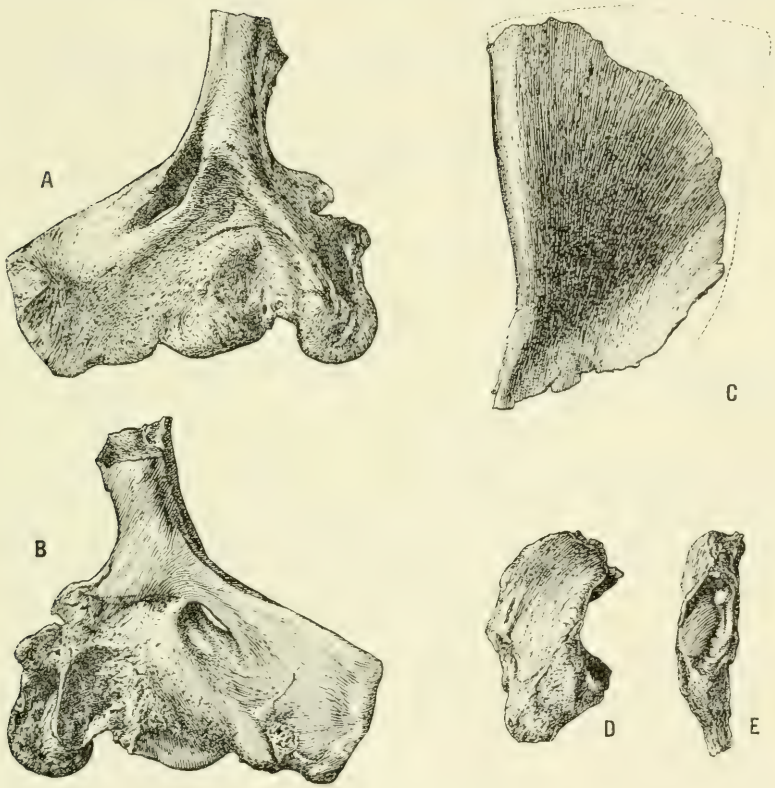


Figure 1. *Clepsydrops magnus* sp. nov. *A, B,* distal end of right humerus, dorsal and ventral surface. *C,* upper part of right scapular blade; probable outline when complete suggested by broken line. *D, E,* lateral and proximal views of upper end of left ulna. All x ½.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS. SEPTEMBER 5, 1961 NUMBER 145

A NEW SPECIES OF THE CETOMIMID GENUS *GYRINOMIMUS* FROM THE GULF OF MEXICO

By Henry B. Bigelow

GYRINOMIMUS PARRI new species

Type. U.S. National Museum No. 196180, from north central part of Gulf of Mexico, 26° 52′ N, 89° 44′ W, OREGON Station 2573. One specimen, 51 mm in standard length.

Distinctive Characters. G. parri differs conspicuously from *G. simplex* Parr 1946,[1] from the Gulf of Mexico, in its relatively much longer dorsal and anal fins, from *G. myersi* Parr 1934,[2] also from the Gulf, in the simple structure of its lateral line pores, and from *G. bruni,* Rofen 1957-59,[3] from the southwestern Indian Ocean, in the number of lateral line pores.

Description. Proportional dimensions in per cent of standard length of the type specimen, 51 mm in standard length.

Snout in front of eye: 51.
Diameter of eye: about 1.
Length of head to pectoral fins: 33.
Snout to origin of dorsal: 62.
Base of dorsal: 24.
Base of anal: 23.
Rear end of base of dorsal to base of caudal: 10.
Length of caudal: 12.
Length of pectorals: 6.
Height at pectorals: 24.
Height at origin of dorsal: 17.
Least height of caudal peduncle: 8.
Height of base of caudal fin: 12

1 Copeia, 1946 : 116, Pl. 1.
2 Bull. Bingham Oceanogr. Coll., *4* (6) : 29, Figs. 8, 9, 1934.
3 Galathea Rept., *1* : 257, 1957-59.

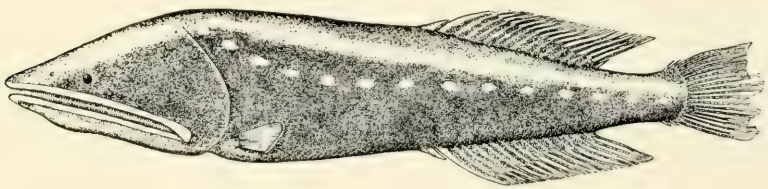
Greatest width between rear end of rami of lower jaw: 18.
Width between upper ends of gill slits: 14.
Dorsal rays: 17.
Anal rays: 17.
Principal caudal rays: 17+ (damaged).
Pectoral rays: 16.

Dorsal profile sloping in nearly a straight line from nape to tip of snout, the latter narrowly rounded vertically but rather broadly rounded transversely; eye minute, much nearer to upper jaw than to dorsal profile; upper jaw projecting a little beyond lower, margins of both jaws weakly concave, the jaws extending rearward about to a perpendicular at upper corner of gill openings. Trunk highest at nape; dorsal profile of body and tail sectors sloping in nearly a straight line from nape to caudal peduncle. Dorsal fin a little higher anteriorly than posteriorly, its margin very weakly convex; anal opposite dorsal and similar to dorsal in outline. Caudal (somewhat damaged) apparently truncate or nearly so; lateral line with 14 large oval pores from nape to base of caudal, the anterior margin of the pores without rearward extending flap. Teeth along entire length of each jaw in 3 continuous rows, those in the row next the gum much the shortest and those in the row farthest from the gum much the longest.

Color. General ground tint sooty black, the eyes blue, the outer parts of the unpaired fins chocolate brown, the teeth ivory white, the inside of the mouth pale gray.

Size. The type (and only known) specimen is 51 mm in standard length.

Range. So far known only from the north central part of the Gulf of Mexico, 26°52′ N, 89°44′ W, OREGON St. 2573, from a trawl haul at 1350 fms.



Gyrinomimus parri n. sp. Type specimen, USNM no. 196180.

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. DECEMBER 14, 1961 NUMBER 146

NEW RODENTS FROM THE EARLY MIOCENE DEPOSITS OF SIXTY-SIX MOUNTAIN, WYOMING

BY CRAIG C. BLACK

Carnegie Museum, Pittsburgh, Pennsylvania

During the summers of 1930, 1931, and 1933, Dr. E. M. Schlaikjer working for the Museum of Comparative Zoology, Harvard University, made a large collection of early Miocene mammals in the southern portion of Goshen Hole, Wyoming. Most of these were obtained from the slopes of Sixty-Six and Bear Creek mountains, from beds that Schlaikjer (1935) interpreted as the Lower Harrison formation.

On two occasions during July, 1959, Sabra B. Black, Laura McGrew, Bryan Patterson, and I made a brief reconnaissance of the area on the western slope of Sixty-Six mountain. During this reconnaissance, it became evident that Schlaikjer's Brule-Lower Harrison contact was actually a local channel conglomerate developed within the early Miocene sediments. He states (1935, p. 112), "At the northwest end of Sixty-Six mountain in the N.E. 1/4, Sec. 7, T.20N., R.60W. the typical Brule clay is overlain by a three-foot clay conglomerate above which are nineteen feet of clay sands that grade upward into the gray sands with pipy concretions." The "typical Brule clay" below the conglomerate, however, is the unit from which the rodents described below were obtained together with a badly weathered *Cyclopidius* skull and jaws and the posterior portions of two rami of *Mesoreodon cheeki*. These specimens were found in place and they clearly indicate an early Miocene, probably Gehring equivalent, age. Below the grey, tuffaceous sand and grading into it are buff clays with some sand which are probably equivalent to the Brule. In this area deposition appears to have been continuous from the Oligocene through the early Miocene with no sharp lithologic or erosional break within this sequence. The clay conglomerate is not extensively developed either on Sixty-Six or Bear mountains and

where it does appear on Sixty-Six mountain it lies within early Miocene sediments as is clearly shown by the oreodonts and rodents described below. A full account of the relationship of the Oligocene and Miocene sediments in the southern part of Goshen Hole is still in progress and will be published at a later date.

I would like to take this opportunity to thank the Kellam family of Torrington, Wyoming, who helped us immeasurably during our stay in the Goshen Hole area. I would also like to thank Professor Bryan Patterson for his criticisms and suggestions. The drawings are by Mr. Clifford J. Morrow and were made possible by a grant from the Gulf Oil Corporation.

Abbreviation used: M.C.Z. — Museum of Comparative Zoology, Harvard University.

Family CRICETIDAE

Scottimus kellamorum[1] n. sp.

Figure 1

Type: M.C.Z. No. 7342, a right maxillary with M^1-M^2.

Hypodigm: Type only.

Horizon and locality: Section 11, T.20N., R.61W., Goshen Co., Wyoming. Arikareean, from the supposed Gehring equivalent, early Miocene.

Diagnosis: Smaller than *Scottimus lophatus;* teeth narrower in relation to length than in *Scottimus exiguus;* antero-posterior lophs more prominent than transverse; protoloph very weak on M^1, absent on M^2; metaloph very weak on M^2, incomplete on M^1.

Description: In general, the upper molars of *Scottimus kellamorum,* like those of *S. lophatus,* are longer and narrower than those of the various species of *Eumys.* The mure is as strongly developed as in *S. lophatus,* but there are more accessory transverse crests than in that species. The cusps on M^1-M^2 are high, and the crests are at a lower level. The anterocone of M^1 is extremely large. There is a connection between the paracone and protocone on M^1, but it is shifted posteriorly and thus does not form a transverse loph. A comparable crest is not present on M^2. The paracone and metacone are joined by a low crest which in turn is joined by the mesolophid. There is a short crest projecting lingually from the mure between the protocone and hypocone on both M^1 and M^2. The anterior cingulum on M^2 is ele-

[1] Named for David and Jean Kellam of Torrington, Wyoming.

vated and strongly developed. The posterior metacone arm on M^1 is directed backward to fuse with the elevated posterior cingulum, whereas on M^2 it passes lingually to the hypocone to form a weak, transverse metaloph.

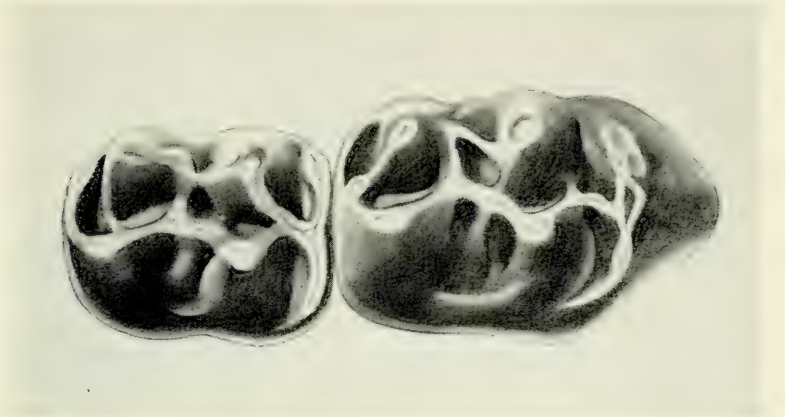


Figure 1. *Scottimus kellamorum* n. sp., Type, M.C.Z. No. 7342, RM^{1-2}, anterior end to the right, X20.

Discussion: Two species of Oligocene eumyines described by Wood (1937) seem referable to *Scottimus*. These are *Eumys exiguus*, from the Middle Oreodon beds of South Dakota, and *Leidymys vetus*, from the Middle Oligocene Cedar Creek beds of northeastern Colorado. Wood (*op. cit.*, p. 254-255), in describing *Eumys exiguus*, stated that it was transitional between typical *Eumys* and *Scottimus*. Galbreath (1953, p. 72) stated that all the specimens referable to *Eumys exiguus* in the University of Kansas collections from the Cedar Creek beds were also "closely similar to the type of *Leidymys vetus* Wood. In fact there is no question in my mind but that they represent the same species." However, he did not synonymize the two, stating, "I think this small species (*Eumys exiguus*) is generically distinct from the species of *Eumys* but am not prepared to say whether or not it should be referred to *Leidymys* or to another genus." Under the circumstances, it seems proper to place *Eumys exiguus* in *Scottimus* and to refer *Leidymys vetus* to the synonymy of this species. This brings the number of recognized species of *Scottimus* to three; *S. lophatus*, *S. exiguus*, and *S. kellamorum*.

In the development of antero-posterior rather than transverse lophs *Scottimus kellamorum* is more advanced than *S. exiguus*. Since *S. exiguus* is of middle Oligocene age this is, of course, to be expected. *S. kellamorum*, however, is not as advanced a species as the earlier *S. lophatus*. The transverse crests seen on M^1 of *S. kellamorum* are also present on *S. lophatus*, but these crests are not seen on M^2 of *S. lophatus*. This would seem to exclude *S. lophatus* from the ancestry of *S. kellamorum;* presumably a species similar to *S. exiguus* was ancestral to both.

Eumys sp.

M.C.Z. No. 7334, a partial left ramus with the incisor and M_1-M_2 cannot be indentified specifically. It does not show any tendency toward the formation of a strong central antero-posterior lophid at the expense of the transverse lophids, and hence is certainly not the lower dentition of *Scottimus kellamorum*. The posterior protoconid arm is extremely elongate on both M_1 and M_2. On M_1, a short anterior metaconid arm just fails to reach the anteroconid whereas a longer protoconid arm does so. In size and general pattern the teeth closely resemble those of *Eumys elegans* and *Eumys obliquidens*. Unfortunately the lower teeth of *Leidymys nematodon* and *lockingtonianus* are unknown.

Family HETEROMYIDAE

Heliscomys schlaikjeri[2] n. sp.

Figure 2

Type: M.C.Z. No. 7335, a right maxillary with P^4-M^2.

Hypodigm: Type only.

Horizon and locality: Section 11, T.20N., R.61W., Goshen Co., Wyoming. Arikareean, from the supposed Gehring equivalent, early Miocene.

Diagnosis: Size larger than that of any other known species of *Heliscomys;* internal cingulum undivided; posterior cingulum on P^4 extending from hypocone to metacone; central transverse valley straight, directed somewhat posteriorly.

Description: No trace of the paracone remains on the anteroloph of the premolar. In this respect, the tooth is typically perognathine. The posteroloph bears three cusps, the metacone

and hypocone being of equal size with the protocone and the entostyle being smaller. The entostyle curves forward and joins the internal edge of the protocone at the same level as does the hypocone. There is a small posterior cingulum running from the hypocone to the base of the metacone, and separated from the posteroloph by a small pit.

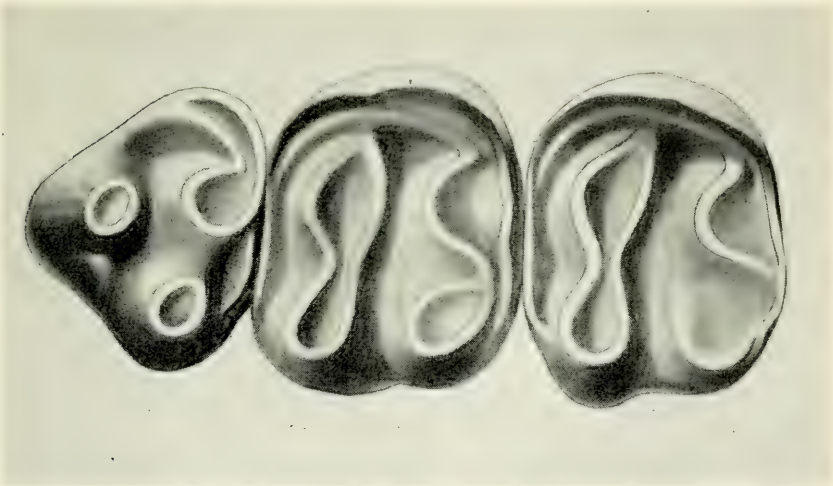


Figure 2. *Heliscomys schlaikjeri* n. sp., Type, M.C.Z. No. 7335, RP^4-M^2, anterior end to the left, X30.

The molars are somewhat more lophate in appearance than are those of *Heliscomys gregoryi* (Wood, 1933) and *H. hatcheri* (Wood, 1935), although the principal cusps are still prominent. In this respect the teeth resemble more closely those of *H. tenuiceps* (Galbreath, 1948). The molars of both agree in having anterior and posterior cingula that rise rather steeply to join the protostyle and entostyle. These cusps are closely appressed with no gap between them, a further point of resemblance to *H. tenuiceps*. The median valley is straight on both teeth, slanting somewhat posteriorly, not sinuous as in *H. gregoryi* and *H. hatcheri*. The anterior cingulum is stronger than the posterior on both M^1 and M^2.

Discussion: Although it is somewhat larger and shows a few minor differences, *Heliscomys schlaikjeri* is extremely close to *H. tenuiceps*. Both species have an undivded internal cingulum

[2] Named for E. M. Schlaikjer in recognition of his extensive work in the Goshen Hole area.

and a straight median valley, characters found neither in *H. hatcheri* nor in *H. gregoryi*. In *H. schlaikjeri*, in addition to the somewhat larger size, the median valley of the molars is directed somewhat more posteriorly and the posterior cingulum on P^4 has shifted position. The latter distinction seems unimportant since the presence or absence and the position of the posterior cingulum are variable in *Heliscomys*. In *H. hatcheri* this cingulum varies from absent to present, in some cases extending along the entire posterior margin of the molars; in a specimen from Pipestone Springs described by McGrew (1941), it appears to be completely absent, while in *H. tenuiceps* it connects the hypocone and the entostyle. Recently, Reeder (1960) has described two new genera of heteromyids from the White River formation and has emphasized their large size and the quadricuspidate nature of P_4 in *Apletotomeus* and the quinquicuspidate P_4 of *Akmaiomys*. These genera are known only on their lower dentitions and hence can not be compared with *H. schlaikjeri*. *H. schlaikjeri*, however, is somewhat larger than either genus.

Table of Measurements (in mm.)

	P^4	M^1	M^2	M_1	M_2
Scottimus kellamorum					
anteroposterior		2.50	1.85		
transverse protoloph		1.60	1.43		
transverse metaloph		1.53	1.35		
Eumys sp.					
anteroposterior				2.10	2.00
transverse metalophid				1.40	1.90
transverse hypolophid				1.70	1.90
Heliscomys schlaikjeri					
anteroposterior	0.90	1.10	1.10		
transverse	1.20	1.40	1.40		

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AUSTRALIAN CARABID BEETLES VIII. *LEIRADIRA*, ESPECIALLY THE TROPICAL SPECIES

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This is the third part of this series to be devoted to flightless Carabidae of zoogeographic importance from tropical eastern Australia. Pertinent earlier parts, including a locality list and a discussion of transition of carabid faunas in wet forests from New Guinea to Tasmania, are listed at the end of the present paper. Information on deposition of types and a brief note on methods will be found at the beginning of Part VI (1961c).

The present paper is concerned with the pterostichine genus *Leiradira*. Typical *Leiradira* are very distinctive Carabidae, distinguished from (for example) *Notonomus* by: deep-bodied form; heavy, sometimes more or less deflexed head, with mandibles somewhat longer and more acuminate than in *Notonomus*; geniculate antennae; mentum tooth absent; and inner lobe of maxilla lined with what look like long slender teeth rather than bristles (see following key). These characters led Tschitschérine (1902, p. 506) to place *Leiradira* in the tribe Deliniini, far removed from *Notonomus*. However, some of my new North Queensland species reduce the gap between *Leiradira* and *Notonomus* and suggest that tribal separation of the two genera may not be justified and that, although the genera are distinct, they (and *Delinius*) may be derived from a common ancestor. This is something to be decided in the future, by the next reviser of the generic classification of Australian Pterostichini.

As I now understand the genus, *Leiradira* (in a broad sense) includes about a dozen species and is discontinuously distributed, chiefly in rain forest, along the eastern edge of Australia from just below Cooktown in tropical North Queensland south at least to the lower edge of the Dorrigo plateau in warm temperate

north-central New South Wales. The genus divides into three well marked subgenera, which have geographical as well as structural bases. They are distinguished in the following key, which includes *Notonomus* for comparison. The tropical species of *Notonomus* will be treated in another paper.

Key to subgenera and some species of Leiradira

1. Mentum tooth normal, long, deeply emarginate; inner lobe of maxilla lined with many coarse setae not in single row; head not deflexed; mandibles shorter; antennae not geniculate, 1st segment shorter than segments 2 + 3; form usually more depressed (but variable) ..... (*Notonomus*)

— Mentum tooth broad and short, or absent; inner lobe of maxilla lined with single row of about 6 to 8 slender teeth; head often (not always) more or less deflexed, with mandibles usually (not always) longer and more acuminate than in *Notonomus;* antennae often (not always) geniculate, with 1st segment usually (not always) as long as or longer than segments 2 + 3; form relatively deep-bodied (*Leiradira, sensu lato*) 2

2. Labrum moderately emarginate, 6-setose; posterior-lateral pronotal setae on thickened margin; (mentum tooth present but broad and short) (North Queensland) (subgenus *Metadira*) 4

— Labrum *either* deeply, almost semicircularly emarginate *or* only 4-setose; posterior-lateral pronotal setae inside (not on) thickened margin; (mentum tooth present or absent) 3

3. Labrum moderately emarginate, 4-setose; mentum without tooth; mandibles shorter, but not so short as in *Notonomus* (northern New South Wales and South Queensland) (*Leiradira, sensu stricto*) ..... 3 or more full species

— Labrum semicircularly emarginate, 6-setose; mentum tooth present (but very broad and short); mandibles longer than usual (South Queensland and Eungella Range) (subgenus *Stomimorphus*) 8

4. Elytral intervals very unequal (odd several times wider than even ones); 1st antennal segment shorter than segments 2 + 3; (color green-purple) ..... *ignifer*

— Elytral intervals less unequal, or equal; 1st antennal segment usually equal to or longer than 2 + 3 5

5. Elytral intervals subequal *and* striae normal, not widened except sometimes near apex 6

— *Either* odd elytral intervals wider than even ones *or* striae partly wide and opaque 7

6. Larger (15-19 mm.); dark blue-purple ..... *alticola*

— Smaller (11-12.5 mm.); black ..... *soror*

7. Odd elytral intervals wider than even ones; elytral striae not much widened; 3rd elytral intervals usually 3- or 4-punctate; scutellar striae weak or obsolete (variable); form more slender ..... *alternans*

— Elytral intervals nearly equal; elytral striae widened and opaque especially behind middle; 3rd elytral intervals always 2-punctate; scutellar striae short but deep; form less slender ..... *opacistriatus*

8. Larger (14.7 mm. or more) ..... *violaceus*

— Smaller (*c.* 10-12 mm.) 9

9. Prothorax wider (W/L 1.14-1.19); duller ..... *jacobi*

— Prothorax narrower (W/L 1.06-1.08); more shining ..... *tennis*

Of the three subgenera, *Metadira* is most like *Notonomus*. Even the least modified *Metadira, aurifer*, differs from *Notonomus* in having a shorter mentum tooth and a regular row of about 8 slender tooth-like processes on inner edge of maxilla instead of more than 20 thickened setae less regularly arranged as in, for example, *Notonomus doddi* Sloane, but there are two indications besides the general similarity that suggest a real relationship. One is the position of the posterior-lateral prothoracic setae, on (not inside of) the thickened margin at basal angles in both *Metadira* and the tropical species of *Notonomus*. The other is the fact that some *Metadira* and some tropical *Notonomus* have elytral striae conspicuously widened and opaque. This is an unusual character, unlikely to have evolved independently in the two genera.

Metadira subgen. n.

Form varying from that of a convex *Notonomus* to that of typical *Leiradira*. *Head* stout, sometimes somewhat deflexed; eyes small, genae prominent (but variable); 2 supraocular setae each side; mandibles varying (in different species) in length and curvature; labrum moderately emarginate, 6-setose; antennae with basal segment varying (in different species) from shorter to longer than next 2 segments together; frontal foveae short but well defined; mentum tooth very short and broad, broadly emarginate; inner lobe of maxilla with single row of setae so thickened as to resemble long slender teeth; palpi slender in both sexes. *Prothorax* cordate, with narrow margins; baso-lateral impressions small but deeply impressed; usual 2 marginal setae each side, posterior ones on thickened margins at basal angles. *Elytra* usually with (sometimes almost without) basal margin; humeri ± dentate; striae entire, narrow or widened (in different species); intervals equal or unequal (in different species); narrow 10th

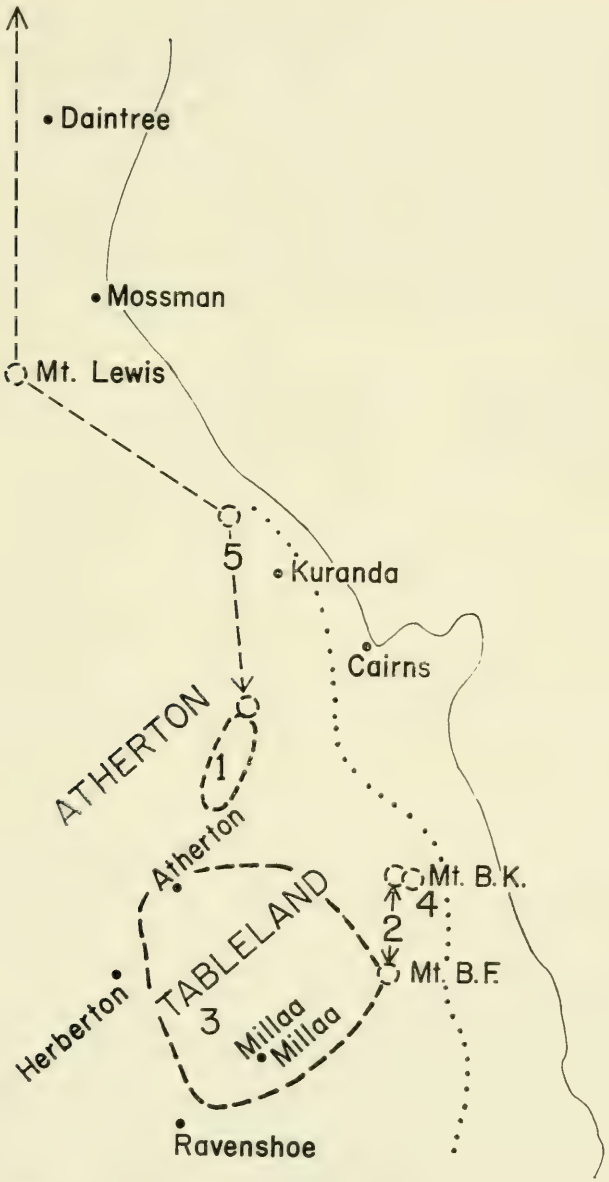
interval present or indicated posteriorly; 3rd interval typically with 2 dorsal punctures (usually only 1 in *alticola* and *soror,* and usually 3 or 4 in *alternans*). Last 3 ventral segments weakly, variably sub-impressed across base but not sulcate; mesosternum and prosternal process not setose. Male with anterior tarsi slightly dilated, 3 segments with squamae; ♂ with 1, ♀ 2 setae each side last ventral segment.

Genotype: *Leiradira aurifer* Darlington (below).

Five species of this subgenus are now known. All occur on (different parts of) the Atherton Tableland/or Mts. Bartle Frere and Bellenden Ker (see map) and the northernmost of the five species extends north nearly to Cooktown. Three of the species (*alternans, soror, opacistriatus*) may be (distinct) geographical forms of one original widely distributed stock (see notes under *alternans*). The other two species are very distinct, localized endemics. All the species are usually found (by day) under cover on the ground, in rain forest, but I got one *opacistriatus* in good savannah woodland a few hundred feet outside rain forest by the Davies Creek Road.

Leiradira (Metadira) aurifer n. sp.

Form as figured (Fig. 1), of a rather convex *Notonomus,* but with characters of *Metadira* as given above; head and pronotum bright green, pronotum with variable purplish reflections, elytra dark copper-purple, lower surface and legs black, mouth parts and antennae brownish; surface shining, except bottoms of striae opaque. *Head* 7/10 or slightly less width prothorax; mandibles shorter than usual in *Leiradira,* rather strongly curved, acuminate apically; eyes moderate (in genus), genae *c.* wide as eyes, weakly rounded to neck; 1st antennal segment *c.* 4/5 (by measurement) length of 2nd + 3rd segments together; middle segments nearly 2X long as wide. *Prothorax c.* 1/10 (±) wider than long at middle, moderately narrowed behind, more in front; base *c.* 1/10 wider than apex; apex subtruncate or very broadly emarginate with angles scarcely advanced, margined only near sides; base slightly sinuously subtruncate, deeply margined toward sides but not at middle; sides broadly rounded for much of length, sinuate near base; basal angles *c.* right, scarcely blunted; disc moderately convex with middle line distinct and reaching base,



Known distribution of *Leiradira*, endemic subgenus *Meladira*, in North Queensland. The finely dotted line is the approximate eastern edge of high land (the Atherton Tableland etc.). No. 1, *aurifer;* 2, *alticola;* 3, *alternans;* 4, *soror;* 5, *opacistriatus,* which occurs also north beyond the limits of the map almost to Cooktown.

transverse impressions almost obsolete, and baso-lateral impressions short, linear, connected with side margins by deeply impressed marginal grooves. *Elytra* ¼ (or slightly more) wider than prothorax; basal margin entire, strongly raised, slightly scalloped, rectangular at subdentate humeri; striae very wide and opaque especially posteriorly; intervals convex, very unequal, odd ones several times wider than even, 7th strongly convex but not sharply carinate at base; a narrow 10th interval present posteriorly; each 3rd interval usually 2-punctate just behind middle and near apex (an additional puncture present near middle on 1 side in 1 specimen). Length 15-19; width 5.0-6.2 mm.

Holotype ♂ (M.C.Z. Type No. 30,382) and 9 paratypes from mountains north of Kairi, Atherton Tableland, North Queensland, 3000-4000 ft., Dec. 1957; and 3 paratypes from south end of Davies Creek road, Atherton Tableland, Dec. 1957; all specimens taken by myself, in rain forest. The two localities are not far apart in the mountain mass that lies on the Atherton Tableland between the Mareeba-Kuranda road on the north and Yungaburra-Lake Barrine road on the south.

See preceding discussion and key for place of this species among other *Leiradira*. Although it has striking specific characters (color, extreme alternation of elytral intervals), it is the least specialized member of the group in form, mandibles, and length of 1st antennal segment.

Leiradira (Metadira) alticola n. sp.

Form as figured (Fig. 2), prothorax strongly cordate, elytra narrowed anteriorly; rather strongly convex; black, usually with purplish tinge, margins of elytra blue; moderately shining. *Head* *c.* ¾ or slightly less width prothorax; mandibles slightly longer and less curved than in *aurifer*; eyes small, genae usually longer and more prominent than eyes, strongly convex; antennae very short, 1st segment slightly longer than next 2 together (by measurement), outer segments scarcely longer than wide. *Prothorax* slightly (less than $\frac{1}{10}$) wider than long at middle; apex truncate with angles scarcely advanced, not margined; base virtually truncate, strongly margined toward sides; sides arcuate for *c.* ¾ of length (sometimes subparallel near middle), strongy sinuate *c.* ⅙ or more of length before base, then parallel or diverging to base; basal angles well defined, right or acute; disc with middle line well impressed, very deep basally, transverse impressions

obsolete, baso-lateral impressions deep, sublinear, connected with side margins by deep basal grooves. *Elytra* c. $^1/_3$ (or slightly less) wider than prothorax, narrowed basally; basal margins entire, scalloped, forming sharply defined right angles at subdentate humeri; striae narrow, slightly wider apically, with a little dull sculpture at bottom; intervals subequal, slightly convex; 3rd interval with 1 puncture near or behind middle, usually without posterior puncture, but latter present on 1 side in 1 individual (see Fig. 2). Parts of lower surface (sides of mesosternum, first ventral segment, and parts of other ventral segments) more or less punctate or subpunctate. Length 15-19; width 5.2-6.5 mm.

Holotype ♂ (M.C.Z. Type No. 30,383) and 3 paratypes from Mt. Bellenden Ker, E. side, 3000-4500 ft., Jan. 1958, and 1 paratype, Mt. Bartle Frere, W. slope, near 5000 ft., Dec. 1957. These 2 mountains are close together at the eastern edge of the Atherton Tableland south of Cairns, North Queensland. All specimens taken by myself, in mountain rain forest.

Distinguished from other *Leiradira* as indicated in the preceding key; unique in form, and notable for very short antennae.

Leiradira (Metadira) alternans Darlington

This species (Fig. 3) was described by me in 1953 (p. 90) from Malanda etc. It is widely distributed on the central-southern Atherton Tableland, the limits of its known distribution being Atherton, Lake Barrine, the lower western slope of Mt. Bartle Frere, and Mt. Fisher southwest of Millaa Millaa. It may be represented by *soror* (below) on the eastern slope of Mt. Bellenden Ker (and perhaps elsewhere on the eastern slope of the Tableland) and by *opacistriatus* on the northern edge of the Tableland and northward.

Leiradira (Metadira) soror n. sp.

Small, slender, convex; shining black with silky lustre but no distinct metallic color. *Head* $^3/_4$ (±) width prothorax; mandibles relatively weakly arcuate; eyes small, genae slightly more prominent than eyes, broadly convex; antennae with 1st segment longer than next 2 together. *Prothorax* narrowly subcordate, as long as or slightly longer than wide; apex subtruncate with angles scarcely advanced, not margined at middle; base subtruncate except slightly rounded toward sides, not margined

except near sides; sides broadly arcuate, subparallel before middle, strongly sinuate about 1/10 of length before base; basal angles *c.* right, scarcely blunted; disc with middle line rather fine but reaching base, transverse impressions weak, baso-lateral impressions nearer sides than middle, linear, deep, joining lateral margins at base. *Elytra* 3/10 (or less) wider than prothorax, subparallel, weakly narrowed anteriorly; basal margin deep, scalloped, rectangular at subdentate humeri; striae fine; intervals convex, subequal; 3rd interval usually 1-punctate slightly behind middle, posterior punctures usually absent (1 present on 1 side in 1 specimen). Parts of lower surface (sides of mesosternum, 1st ventral segment, parts of other ventral segments) variably punctate. Length 11.0-12.5; width 3.3-3.7 mm.

Holotype ♂ (M.C.Z. Type No. 30,384) and 2 paratypes all from E. side Mt. Bellenden Ker, *c.* 3000 ft., North Queensland, Jan. 1958, taken by myself in rain forest.

This species most resembles *alternans* (above) but is smaller, narrower, with less alternation of elytral intervals, and fewer punctures on 3rd elytral interval.

Leiradira (Metadira) opacistriatus (Sloane)

Sloane first (1902, p. 319) described this species in *Notonomus*, then (1913, p. 409) ruled it out of that genus. The types were said to be from Cairns, collected by Froggatt; they probably really came from the mountains near Cairns. I could not locate the types in Australia, but my specimens fit the description reasonably well. They are from the Davies Creek road on the northern Atherton Tableland; near Black Mt. about 20 miles north of Kuranda (these are probably virtual topotypes); Mt. Lewis southwest of Mossman; and Mt. Finnegan south of Cooktown.

Leiradira, *sensu stricto*

Castelnau 1867, p. 72.

Csiki 1929, p. 500 (see for additional references and list of previously described species).

Genotype, by present designation: *Leiradira auricollis* Castelnau (Fig. 4) (genus originally based on this species and *latreillei* Castelnau).

Leiradira, sensu stricto apparently occurs only below the tropics, from the Blackall Range etc. in South Queensland south at least to the lower (eastern) edge of the Dorrigo plateau. The

subgenus includes at least three full species, perhaps more. I have not studied them and cannot establish synonymies.

Subgenus Stomimorphus Straneo

Straneo 1953, p. 1.

Leiradira-like Carabidae with mandibles long, acuminate; labrum deeply emarginate, 6-setose; mentum tooth present but short, broad; antennae with 1st segment longer than 2nd + 3rd together; posterior-lateral setae of pronotum inside thickened margin.

Genotype: *Stomimorphus violaceus* Straneo.

This subgenus is apparently confined to southern and central eastern Queensland. The type locality of *violaceus* is simply Queensland. I have what may be this species from Maleny, on the Blackall Range, and additional, smaller species are described here from Mt. Jacob and the Eungella Range.

Leiradira (Stomimorphus) violaceus (Straneo)

Straneo 1953, p. 1.

Described as violaceous; length 14.7 by 4.9 mm. The unique type is a ♂ from "Australia, Queensland" in the Straneo Collection. Two specimens that I collected near Maleny, on the Blackall Range, South Queensland, in rain forest, are greenish violaceous and larger than the type, but I hesitate to describe them without more material to show extent of variation.

Leiradira (Stomimorphus) jacobi n. sp.

Form as figured (Fig. 5); labrum, mentum tooth, and other characters as described for *Stomimorphus;* head and prothorax greenish black, elytra purplish darker dorsally, lower surface and appendages dark; moderately shining, elytra slightly duller and with distinct, fine reticulate microsculpture. *Head* not quite ¾ (*c.* .72) width prothorax. *Prothorax* subcordate, slightly less than ⅓ wider than long at middle, width/length 1.14-1.19; apex subtruncate; base slightly emarginate at middle and rounded toward sides; base and apex not distinctly margined; sides broadly rounded for most of length, slightly sinuate before base; basal angles slightly obtuse, slightly blunted; disc convex, middle line fine, transverse impressions weak, baso-lateral impressions linear, moderately impressed, not punctate. *Elytra* ¼ (or more)

wider than prothorax, slightly narrowed anteriorly; basal margins entire, forming obtuse-right angles at humeri; latter finely bluntly subdentate; striae moderately impressed, entire, not punctate; dorsal intervals equal, slightly convex; 10th interval present posteriorly; 3rd intervals 2-punctate in all specimens, near middle and posterior ¾ (but position of punctures slightly variable). Secondary sexual characters normal, i.e. ♂ with anterior tarsi slightly dilated with 3 segments squamulose below; and ♂ with 1, ♀ 2 setae each side apex last ventral segment. Length 9.8-12.0; width 3.3-4.1 mm.

Holotype ♂ (M.C.Z. Type No. 30,385) and 9 paratypes all from Mt. Jacob, *c.* 45 miles south of Gladstone, South Queensland, *c.* 2000 ft. altitude, Mar. 1958, taken by the Darlingtons, in rain forest.

Superficially this species is deceptively similar to *Leiradira, sensu stricto,* but the species' technical characters are as in *Stomimorphus.*

Leiradira (Stomimorphus) tenuis n. sp.

Form as figured (Fig. 6); with characters of *Stomimorphus* as here given; dark purplish, lower surfaces and appendages dark; shining, elytra with faint fine microreticulation. *Head* ¾ or slightly less width prothorax. *Prothorax* narrow, width/length 1.06-1.08 (all specimens); apex subtruncate or very broadly emarginate; base broadly emarginate at middle, slightly rounded toward sides; base and apex not distinctly margined; sides weakly arcuate for much of length, slightly sinuate near base; disc with fine middle line, very weak transverse impressions, moderate linear baso-lateral impressions, not punctate. *Elytra c.* ⅓ wider than prothorax; basal margin entire, forming slightly obtuse (nearly right) angles at humeri; latter bluntly subdentate; striae entire, moderately impressed, not punctate; intervals slightly convex, subequal; 10th interval present posteriorly; 3rd interval 2-punctate, near middle and apical ¾. Length 10.0-11.5; width 3.3-3.5 mm.

Holotype ♀ (M.C.Z. Type No. 30,386) and 2 ♀ ♀ paratypes all from the Eungella Range, west of Mackay, Queensland, 2000-3000 ft., Nov. 1957, taken by the Darlingtons, in rain forest.

This resembles and may be related to *jacobi* (above) but the prothorax of the present species is narrower and the elytra more shining.

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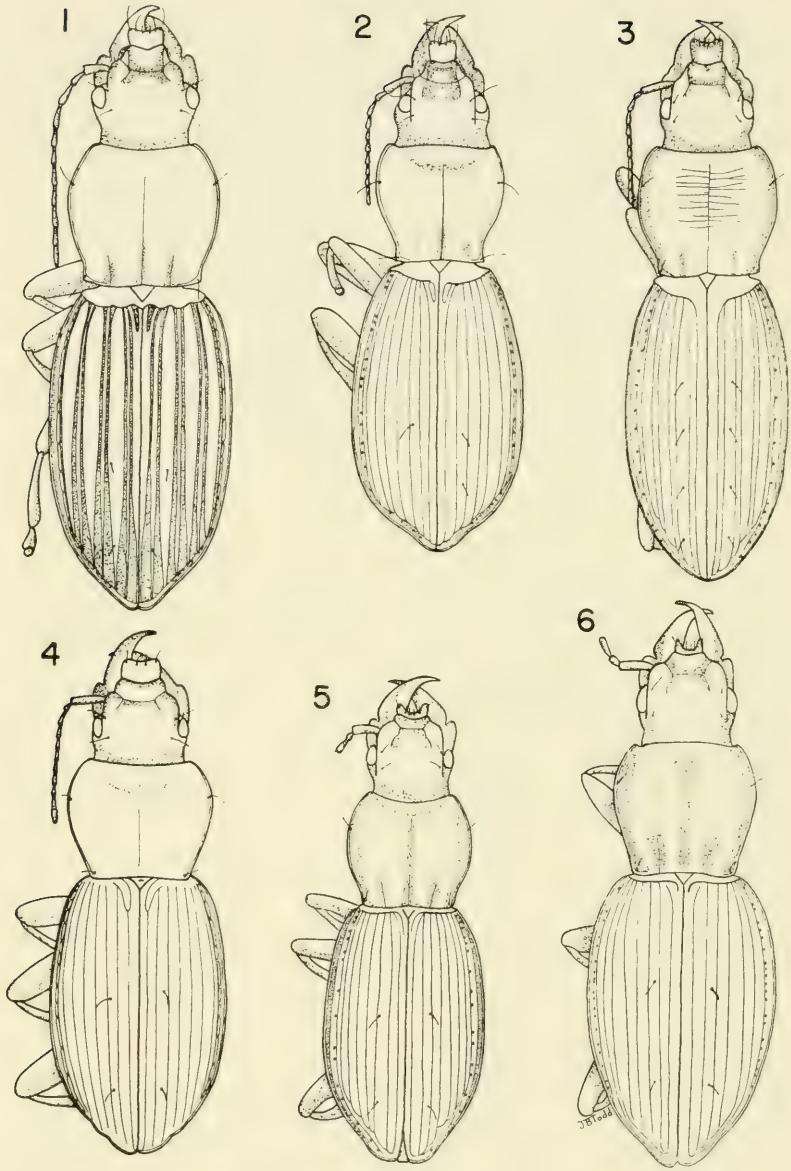

Fig. 1. Leiradira (Metadira) aurifer n. sp.
Fig. 2. Leiradira (Metadira) alticola n. sp.
Fig. 3. Leiradira (Metadira) alternans Darlington
Fig. 4. Leiradira (*sensu stricto*) auricollis Castelnau
Fig. 5. Leiradira (Stomimorphus) jacobi n. sp.
Fig. 6. Leiradira (Stomimorphus) tenuis n. sp.

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AUSTRALIAN CARABID BEETLES IX. THE TROPICAL *NOTONOMUS*

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This is the last of four papers on flightless Carabidae of zoogeographic importance from tropical eastern Australia — but these papers are part of my general series on Australian carabid beetles, which will be continued. Pertinent earlier parts of the series, including a locality list (with maps) and a discussion of the transition of wet forest carabid faunas from New Guinea to Tasmania, are listed with references at the end of the present paper. Information on deposition of types will be found at the beginning of Part VI (1961c). In this as in other parts of this series, proportions stated as simple fractions are based on actual measurements made with a ruled ocular in the microscope.

The present paper concerns the tropical species of the dominant eastern Australian pterostichine genus *Notonomus*. The genus as a whole ranges along the eastern edge of Australia from the base of the Cape York Peninsula (somewhere between Daintree and Cooktown) to Victoria and Tasmania in the south, extending west into the eastern edge of South Australia, with one very distinct species geographically isolated in southwestern Australia and two species described from New Caledonia. I have dealt with some of the tropical Australian species before (1953) but several additional species are now to be described and a new key is necessary.

The tropical species of *Notonomus* are all apparently related among themselves and form what may be called the *doddi* subgroup of Sloane's (1913) *kingi* group of the genus. The *doddi* subgroup is characterized by posterior-lateral setigerous punctures of pronotum on (not inside) thickened margin at basal angles; elytra fully and strongly striate; 3rd interval not more than (but sometimes less than) 2-punctate (except that rarely

individuals have extra adventitious punctures) and 5th and 7th intervals impunctate; 8th interval (10th in *saepistriatus*) narrow and convex (least so in *masculinus*); metepisterna short; intercoxal declivity of prosternum flat, without setae; tarsi not striolate above; posterior tarsi with 1st segment rather long (but not quite so long as next 2 together) and with claw segment glabrous below; and ♂ with 1, ♀ usually 2 setae each side last ventral segment (1 seta each side in ♀ *montellus*, and single anal setae may be either missing or duplicated in individuals of other species), and ♂ with anterior tarsi dilated with 3 segments squamulose below, ♀ *usually* with tarsi unmodified (but some [not all] ♀♀ of *doddi, flos, montorum,* and *masculinus* have front tarsi with 1st segment squamulose). Other characters common to all members of the *doddi* subgroup, and therefore not repeated in the following brief descriptions, are: prothorax with apex subtruncate or broadly emarginate with angles not or not much advanced beyond arc of emargination, margined at sides but not at middle; base slightly sinuously subtruncate, margined only at sides; side margins rather narrow, only slightly wider posteriorly; disc with middle line nearly entire, transverse impressions weak or obsolete, baso-lateral impressions long, linear, moderately impressed, not punctate; elytra with basal margin *c.* rectangular at finely subdentate humeri; narrow extra (10th, or 12th in *saepistriatus*) submarginal interval present at least posteriorly. Although they agree in these characters (with exceptions noted), the species of the *doddi* subgroup differ remarkably among themselves in some other characters, given in the following key.

Explanation of Map on Page 3

Known distribution of *Notonomus* in tropical Queensland. The finely dotted line is the approximate eastern edge of high land (the Atherton Tableland etc.). No. 1 (arrow) indicates occurrence of *Notonomus transitus* endemic on the Eungella Range south of the limits of the map; 2, *N. doddi* in the Herberton-Atherton area, and also (arrow) south of the limits of the map on the Kirrama Range, the Mt. Fox plateau, and the Mt. Spec plateau; 3, *montellus;* 4, *dimorphicus;* 5, *spurgeoni;* 6, *flos;* 7, *montorum* with subspecies *azul* on Mt. B(ellenden) K(er); 8 (arrow) *ellioti,* endemic on the Elliot Range south of Townsville, beyond limits of map; 9, *masculinus;* 10, *saepistriatus.* Note the wide gap between the Atherton Tableland species and those on the mountains of the Mossman-Daintree area; the 3 species on the latter mountains are apparently derived from one secondary ancestor.

Distribution of tropical *Notonomus*.

So far as I know, all the tropical *Notonomus* are confined to rain forest, and they *may* all be derived from a single primary ancestor that invaded tropical rain forest from the more southern part of eastern Australia. *N. transitus,* on the Eungella Range in east-central Queensland, may be a (presumably modified) derivative of this ancestor. Of the more northern species (see map), *doddi* of the Dividing Range system from Mt. Spec to Atherton, and *montellus* of Mts. Bartle Frere and Bellenden Ker, may be related to each other; *montorum,* of Mts. Bartle Frere and Bellenden Ker, and *ellioti,* of the Elliot Range south of Townsville, may be relicts of one more widely distributed secondary ancestor; *masculinus* and *sacpistriatus,* with allopatric ranges on the Atherton Tableland, may be related to each other in spite of their structural differences; and the three species north of the Atherton Tableland (*dimorphicus, flos, spurgeoni*) may be interrelated and may now be in process of radiation from one secondary ancestor. All this suggests the probable complexity of evolution of the group in the rain forests of North Queensland, especially on and near the Atherton Tableland. The radiation of *Trichosternus* in the same area (Darlington 1961d) may have been even more complex. Incidentally, no species of either *Notonomus* or *Trichosternus* has yet been found on the heavily rain-forested mountains that lie on the northern part of the Atherton Tableland between the Yungaburra-Lake Barrine road (on the south) and the Mareeba-Kuranda road (on the north), although these mountains are the home of a striking endemic *Leiradira* (*aurifer* Darlington 1961e).

Key to tropical species of NOTONOMUS (*doddi subgroup*)

1. Species with *all* following characters: elytral striae not widened on disc, and intervals normal in number and not much interrupted, and 3rd interval with dorsal punctures 2

— *Either* striae wide and opaque on disc (not just on declivity), *and/or* intervals more numerous or much interrupted, *and/or* 3rd interval without dorsal punctures 7

2. Sides of ventral segments 4-6 extensively punctate (more so than 1st ventral); (dull black, pronotum virtually smooth) ..... *transitus*

— Ventral segments not punctate or, if punctate, 1st most strongly so 3

3. Pronotum deeply and closely transversely strigulose 4

— Pronotum only normally (lightly or faintly) transversely strigulose ... 5

4. Brownish black, usually larger (12.5-16 mm.); ♀ with 2 setae each side last ventral segment ..... *doddi*

— Bluish or purplish; usually smaller (10.5-13 mm.); ♀ with 1 seta each side last ventral ..... *montellus*

5. Male slender (Fig. 3) (♀ less so); (bicolored) ..... *dimorphicus*

— Both sexes stouter 6

6. Wholly purplish or bluish; length *c.* 12-17 mm. ..... *spurgeoni*

— Bicolored, head and pronotum purple or coppery, elytra black; broader and larger, length *c.* 16-20 mm. ..... *flos*

7. Elytral intervals not much interrupted (3rd without dorsal punctures) 8

— Elytral intervals much interrupted (3rd with or without dorsal punctures 9

8. Form broader; dull ..... *montorum*
   a. Greenish or purplish ..... *montorum, sensu stricto*
   b. Bluish with elytral margins bright blue ..... subsp. *azul*

— Form narrower; more shining, purplish ..... *ellioti*

9. Elytron with 9 intervals, without dorsal punctures ..... *masculinus*

— Elytron with 11 intervals plus narrow submarginal one posteriorly (7th interval tripled), and with dorsal punctures ..... *saepistriatus*

Notonomus transitus n. sp.

With characters of *doddi* subgroup; form as figured (Fig. 1), rather broad and depressed (in group); black, upper surface sometimes slightly aeneous, marginal channels of elytra usually cupreous or dull greenish; most of upper surface with fine isodiametric microsculpture. *Head* ⅔ or slightly less width prothorax, without noticeable unusual characters. *Prothorax c.* ¼ or less wider than long; sides weakly arcuate for most of length, slightly sinuate almost at base; basal angles slightly obtuse, not much blunted; disc smoother than usual, with transverse strigulation very faint or absent. *Elytra* slightly less than ⅕ wider than prothorax; striae rather fine, not punctate, not widened even on declivity; intervals nearly flat on disc, more convex laterally, the discal ones subequal; 3rd interval 2-punctate, behind middle and behind apical ¾. Lower surface nearly impunctate anteriorly but much of abdomen finely and closely but rather irregularly punctate. Secondary sexual characters normal; all ♀♀ (16) with simple anterior tarsi. Length *c.* 13-18; width 4.5-6.1 mm.

Holotype ♂ (M.C.Z. Type No. 30,387) and 26 paratypes all from the Eungella Range, west of Mackay, east-central Queensland, 2000-3000 ft. altitude, Nov. 1957, taken by the Darlingtons, in rain forest.

Superficially, *transitus* is similar to the common, variable *N. nitidicollis* Chaudoir of South Queensland. There may be a real relationship between these two species. However, *transitus* leads toward the North Queensland species of the genus in position of the posterior-lateral prothoracic setae, on the thickened margin (inside the margin in *nitidicollis*), and it differs from *nitidicollis* in other specific characters. For example, *transitus* is broader and more depressed, with flatter elytral intervals than *nitidicollis*, and the extensive punctation of the abdomen of *transitus* is lacking in *nitidicollis*. The northern limit of *nitidicollis*, incidentally, is probably Mt. Jacob, about 45 miles south of Gladstone, South Queensland. Of the North Queensland species, *transitus* is probably nearest *doddi* but differs in being broader and more depressed, with flatter elytral intervals, without special pronotal sculpture, but with abdominal punctation.

Notonomus doddi Sloane

The type locality is the Herberton District, Atherton Tableland, North Queensland (Sloane 1913, p. 439). Specimens that I collected on the mountains south and west of Atherton (between Atherton and Herberton) are virtually topotypes. The species extends south (discontinuously) along the Dividing Range system to the Kirrama Range, the Mt. Fox plateau, and the Mt. Spec plateau not far north of Townsville.

The exceptionally close and deep transverse strigulation of the pronotum is apparently always present in this species, but the other pronotal microsculpture is dimorphic. Most individuals have the head very finely and the elytra more coarsely (but still finely) isodiametrically reticulate and the pronotum *longitudinally* roughened between the deep transverse strigae. However, my series of 11 specimens from the Mt. Spec plateau includes 3 ♂♂ with pronotum without longitudinal roughening, although the 4 other ♂♂ and all 4 ♀♀ have the roughening present, as do all specimens from other localities. The length of this species is *c.* 12.5-16.5 mm., with the average size decreasing southward.

Notonomus montellus n. sp.

With characters of *doddi* subgroup as given above; form as figured (Fig. 2), small, slightly depressed; bluish or purplish black; head and elytra with fine isodiametric microsculpture, less distinct on pronotum. *Head* ⅔ or slightly less width prothorax, without obvious unusual characters. *Prothorax* ⅕ (±)

wider than long; sides broadly arcuate for most of length, briefly sinuate before *c.* right, scarcely blunted basal angles; main (central) part of disc with many deeply impressed, close-spaced, slightly irregular, transverse strigae; surface of disc otherwise not distinctly punctate. *Elytra* ¼ (±) wider than prothorax; striae well impressed, not punctate, not or scarcely widened even on declivity; intervals moderately convex, subequal on disc; 3rd 2-punctate near middle and apical ¼ (punctures slightly variable in position). Lower surface with a little scattered (variable) punctation especially on sides of mesosternum and 1st ventral segment. Secondary sexual characters normal except ♀ with 1 seta (not 2) each side last ventral segment. Length *c.* 10.5-13.0; width 3.5-4.4 mm.

Holotype ♂ (M.C.Z. Type No. 30,388) and 5 ♂♂ 4 ♀♀ paratypes from Mt. Bartle Frere, west slope, 3000-5000 ft., Dec. 1957; and 1 additional ♀ (not a type) from Mt. Bellenden Ker, east side, about 4500 ft., Dec. 1957. These two mountains are close together at the east side of the Atherton Tableland, south of Cairns, North Queensland. Specimens all taken by the Darlingtons, in mountain rain forest.

This small *Notonomus* is closest in technical characters to *N. doddi* Sloane, of the Dividing Range system, and may be related to it, but differs in smaller size, more depressed form, color, and presence of only 1 seta each side ♀ last ventral segment. The pronotal sculpture resembles that of the exceptional *doddi* from Mt. Spec, with deep transverse strigulation but without longitudinal roughening.

Notonomus dimorphicus n. sp.

With characters of *doddi* subgroup as given above; ♂ (Fig. 3) exceptionally slender, ♀ (Fig. 4) less so; head and prothorax aeneous, elytra purplish black; moderately shining with fine isodiametric microsculpture on head and elytra, not distinct on pronotum. *Head c.* ¾ or more width prothorax, without noticeable unusual characters. *Prothorax* slightly longer than wide in slender ♂♂, slightly wider than long in stouter ♀♀ (but slightly variable in both sexes); sides rather weakly rounded, in ♂♂ nearly straight and converging both before and behind submedian curve but more regularly arcuate in ♀♀; sides briefly, variably sinuate just before base; basal angles right or slightly obtuse, not much blunted; surface of disc with faint transverse strigae, not punctate. *Elytra c.* ⅕ (±) wider than prothorax;

striae not widened except slightly so (striae 1 and 2) at extreme apex, on declivity; intervals moderately convex, not interrupted, subequal on disc; 3rd 2-punctate, near middle and posteriorly (middle puncture sometimes duplicated). Lower surface nearly impunctate. Secondary sexual characters (other than dimorphism of form) normal. Length *c.* 12-15; width 3.6-4.6 mm.

Holotype ♂ (M.C.Z. Type No. 30,389) and 7 ♂♂, 7 ♀♀ paratypes all from Mt. Lewis, near Mossman, North Queensland, *c.* 3000 ft., Dec. 1957, collected by the Darlingtons, in rain forest.

Males of this species are unique in form at least among the tropical species of the genus, and at first I thought they might represent transition toward *Leiradira*, but the mandibles, antennae, and setae of the inner edge of the maxilla are as usual in *Notonomus*. The ♀♀ are close to *N. spurgeoni* (below) but are more slender and bicolored. All specimens that I refer to the present species were taken within a comparatively small area of continuous mountain forest, and I feel sure they represent a single population. A single ♀ that I refer to *spurgeoni*, although labeled from Mt. Lewis, may have been taken outside of and below the area occupied by *dimorphicus*.

Notonomus spurgeoni Darlington

This is the most northern known species of *Notonomus*. I described it (1953, p. 98) from a series from Mt. Spurgeon, about 12 miles northwest of Mt. Lewis in the same mountain system. Three specimens from Thornton Peak, northeast of Daintree, near 4000 ft., Dec. 1957, taken by the Darlingtons in mountain rain forest, seem to be the same species, although the color is bluish rather than purplish. A single ♀ from Mt. Lewis is also apparently referable to this species (see note under *dimorphicus,* above).

Notonomus flos n. sp.

With characters of *doddi* subgroup as given above; form as figured (Fig. 5), rather large and broad in group; black, head and pronotum bright violaceous or cupreous; moderately shining, elytra slightly duller; fine isodiametric microsculpture very distinct on elytra, absent or indistinct on head and pronotum. *Head* ⅔ (±) width prothorax, without obvious unusual characters. *Prothorax* large, ⅕ to ⅓ wider than long; sides broadly arcuate for almost entire length, usually minutely sinuate at base (the sinuation involves hardly more than widening of the marginal

bead); basal angles obtuse (sometimes nearly right); surface of disc with weak transverse strigae. *Elytra* slightly wider than prothorax; striae well impressed, not punctate, not or not much widened on disc but inner ones wider and dull on declivity; intervals convex, subequal on disc; 3rd 2-punctate near middle and posteriorly (exact position of punctures variable as usual). Lower surface nearly impunctate. Secondary sexual characters normal except some ♀♀ (2 of 4) with front tarsi with 1st segment squamulose below, although not dilated. Length *c.* 16-20; width 5.5-6.4 mm.

Holotype ♂ (M.C.Z. Type No. 30,390) and 17 paratypes (13 ♂♂, 4 ♀♀) all from Mt. Lewis, southwest of Mossman, North Queensland, *c.* 3000 ft., Dec. 1957, taken by the Darlingtons in mountain rain forest.

The comparatively large, broad form, color, and characters given in the key should easily distinguish this species. It was found with *dimorphicus* on Mt. Lewis, and the occurrence of *spurgeoni* too there or nearby raises an interesting problem of speciation. I think all 3 species have probably been derived from one ancestor, but I do not know how the divergence has come about.

Notonomus montorum n. sp.

With characters of *doddi* subgroup as given above; form as figured (Fig. 6), rather large, broad, and depressed in group; greenish or sometimes vaguely purplish with elytral margins usually greenish and never bright blue; rather dull, entire upper surface with very fine, isodiametric reticulate microsculpture. *Head c.* ⅔ width prothorax, without noticeable unusual characters. *Prothorax* ¼ to ⅓ wider than long; sides broadly arcuate for much of length, usually broadly but slightly sinuate posteriorly; basal angles usually subprominent, *c.* right, scarcely blunted; surface of disc with weak transverse strigulae. *Elytra c.* ⅓ or more wider than prothorax; striae widened and opaque especially posteriorly; intervals moderately convex, subequal on disc; 3rd without dorsal punctures. Lower surface with sides of ventral segments (especially 1st) finely and irregularly punctate, but sterna nearly impunctate. Secondary sexual characters of ♂♂ and most ♀♀ normal, but exceptional ♀♀ with 1st segment front tarsi with squamae below. Length *c.* 15.5-19.5; width 5.2-6.9 mm.

Holotype ♂ (M.C.Z. Type No. 30,391) and 76 paratypes from Mt. Bartle Frere, west slope, 3000-5000 ft., Dec. 1957, and 12 additional paratypes with the same data except 2000-3500 ft. altitude; all specimens taken by the Darlingtons, in mountain rain forest. Mt. Bartle Frere is at the eastern side of the Atherton Tableland south of Cairns, North Queensland. A weak subspecies (below) occurs on neighboring Mt. Bellenden Ker.

See key for distinguishing characters of this species, and see also note under *ellioti* (below).

Notonomus montorum azul n. subsp.

Structurally similar to typical *montorum* (above) but more shining and different in color, bluish black with elytral margins bright blue in all specimens. Of 5 ♀♀, 1 has and 4 have not squamae on 1st segment of front tarsi. Length *c.* 16-19; width 5.3-6.6 mm.

Holotype ♂ (M.C.Z. Type No. 30,392) and 11 paratypes all from Mt. Bellenden Ker, east side, 3000-4500 ft., Jan. 1958, collected by myself in mountain rain forest. Mt. Bellenden Ker is about 10 miles north of Mt. Bartle Frere at the eastern edge of the Atherton Tableland south of Cairns, North Queensland.

Notonomus ellioti n. sp.

With characters of *doddi* subgroup as given above; form as figured (Fig. 7), narrower than *montorum*, moderately depressed; purplish black, rather shining; fine reticulate microsculpture present but lightly impressed on head and pronotum, slightly more distinct on elytra. *Head* ⅔ or slightly less width prothorax, without noticeable unusual characters. *Prothorax c.* ⅕ or slightly less wider than long; sides broadly, rather weakly arcuate for most of length, then slightly sinuate near base; basal angles *c.* right, well defined; disc faintly, transversely strigulose (as in most species of genus). *Elytra c.* ⅕ or less wider than prothorax; striae narrow anteriorly but widening on posterior part of disc and especially on declivity; intervals moderately convex, subequal on disc (odd ones slightly wider than even); 3rd without dorsal punctures. Lower surface almost impunctate. Secondary sexual characters normal in ♂; ♀ unknown. Length *c.* 16-18; width 5.0-6.0 mm.

Holotype ♂ (M.C.Z. Type No. 30,393) and 5 paratypes (all ♂♂) all from the Elliot Range (actually from near the summit

of "Sharp Elliot"), *c.* 3000 ft., Mar. 1958, taken by my son and myself in mountain rain forest.

This species may be related to *montorum* of Mts. Bartle Frere and Bellenden Ker. If so, the two mountain species are presumably relics of a once more widely distributed stock. As compared with *montorum*, the present species is more slender, with elytral striae narrower, especially anteriorly.

Notonomus masculinus Darlington

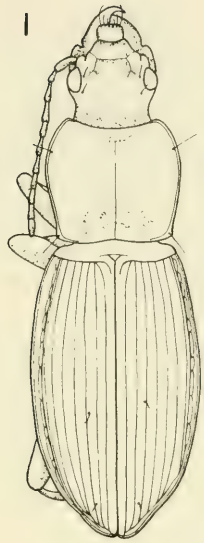
N. masculinus (Fig. 8) is a relatively large, broad species with elytral intervals normal in number but heavily catenulate (much interrupted) and without dorsal elytral punctures. It has an extensive distribution on the southern part of the Atherton Tableland. I described it (1953, p. 99) from Millaa Millaa, and other known localities are indicated below. I have noted elsewhere (1961c, p. 7) the resemblance between this species and *Pamborus punctatus*, and have suggested that it may be a case of mimetic convergence.

In ♂♂ of *masculinus* the front tarsi are moderately dilated, with three segments squamulose below. In some ♀♀ the front tarsi are normal (without squamae) but in others the front tarsi, though scarcely widened, have the 1st segment biseriately squamulose. My single ♀ from Millaa Millaa has the front tarsi squamulose as described, and so does the single ♀ from Herberton. A single ♀ from between Millaa and Innisfail has the tarsi simple. In a series of specimens from mountains (including Mt. Fisher) between Millaa Millaa and Ravenshoe, 5 ♀♀ have tarsi simple, 3 squamulose. Three ♀♀ from Longlands Gap all have simple tarsi. My single specimen from the western foot of Mt. Bartle Frere (the northeastern known limit of the species' range) is a ♂.

Notonomus saepistriatus Sloane

triplicatus Darlington 1953, p. 100 (new synonymy).

Sloane (1907, p. 364) described this species (Fig. 9) from Atherton, on the Atherton Tableland, North Queensland. I misinterpreted Sloane's description and re-described the species from Lake Barrine and Yungaburra, on the Tableland not far from the type locality. In 1957-1958 my wife, son, and I took a total of 8 more specimens of the species at Atherton, Yungaburra, and Lake Eacham. At Atherton, we found it only in patches of rain forest on the flat part of the Tableland along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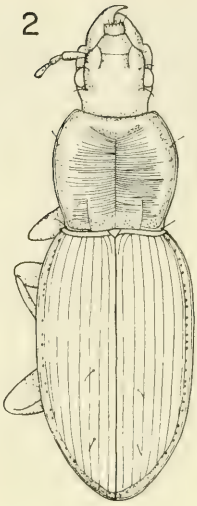
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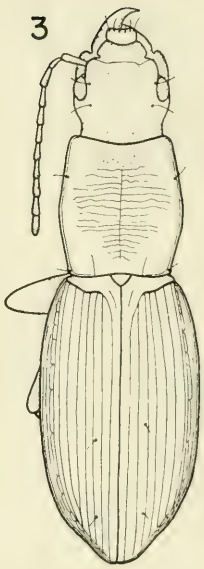
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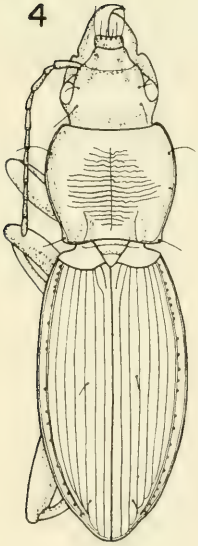
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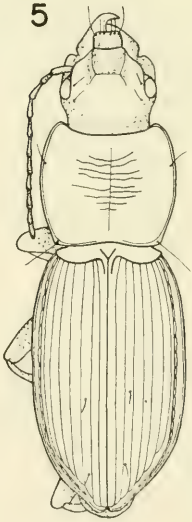
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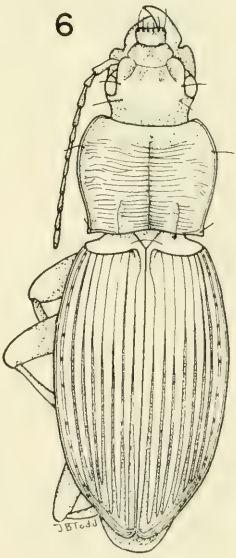
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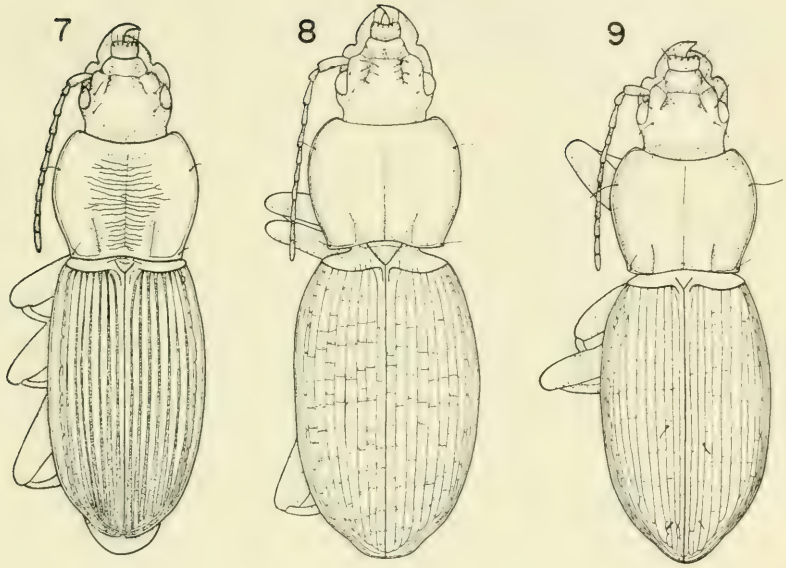

Fig. 1. Notonomus transitus n. sp.
Fig. 2. Notonomus montellus n. sp.
Fig. 3. Notonomus dimorphicus n. sp. (slender ♂).
Fig. 4. Notonomus dimorphicus n. sp. (♀).
Fig. 5. Notonomus flos n. sp.
Fig. 6. Notonomus montorum n. sp.
Fig. 7. Notonomus ellioti n. sp.
Fig. 8. Notonomus masculinus Darlington
Fig. 9. Notonomus saepistriatus Sloane

the road toward Mareeba. The species, therefore, seems to be uncommon, confined to a very limited area (a strip about 10 miles long) of the central Atherton Tableland. It apparently does not occur in the mountains west and south of Atherton, where it is replaced by *doddi*, and does not overlap the range of *masculinus*. In other words, these 3 strikingly different species seem to be allopatric. My 3 ♀♀ of *saepistriatus* all have narrow, unclothed front tarsi.

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BREVIORA

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A PRELIMINARY STUDY OF THE SILURIAN CERATIOCARIDIDS (CRUSTACEA: PHYLLOCARIDA) OF LESMAHAGOW, SCOTLAND

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AND

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The following ten species of *Ceratiocaris* have been recorded by Peach (1901, pp. 450-451) and Jones and Woodward (1888b, p. 72) from beds of uppermost Valentian age in the Lesmahagow inlier, Lanarkshire, Scotland:

C. inornata M'Coy, 1851
**C. angusta* Etheridge, Woodward and Jones, 1886b
**C. laxa* Etheridge, Woodward and Jones, 1886b
C. longa Jones and Woodward, 1885
C. murchisoni (Agassiz), 1837
**C. papilio* Salter, 1859
**C. stygia* Salter, 1860
C. patula Etheridge, Woodward and Jones, 1888
C. robusta Salter, 1860
C. attenuata Etheridge, Woodward and Jones, 1886b
[=*C. tyrannus* Salter *in* Etheridge and Newton, 1878, *nom. nud.*]

Species indicated by an asterisk are based on type specimens from Lesmahagow. It is unlikely that ten sympatric species of *Ceratiocaris* would be ecologically compatible (Gause's principle — see also Simpson, 1961, p. 74), and examination of the supposedly diagnostic characters of these species suggests that the majority

are mere variants. Thus *C. inornata* is stated by Jones and Woodward (1885, p. 394; 1886a, p. 343; 1888b, p. 37) to "agree perfectly in form and proportions [of the carapace] with *C. papilio* from Lesmahago, also in ornament, except that the postero-dorsal convergence of the striae is not present." Yet elsewhere they state that the *C. inornata* from Lesmahagow (BM 59648) is "near to *C. papilio* in form" but that its "proportions are different from those of *C. papilio*" (1885, pp. 460-461; 1886a, p. 346; 1888b, p. 49). My own measurements (W.D.I.R.) on this specimen differ from those given by Jones and Woodward, but even if their values are taken the proportions are found to be identical with the figured specimen of *C. papilio* provided by Jones and Woodward (1885, pl. 10, fig. 1; 1888b, pl. 12, fig. 1). The specimen is too poorly preserved to distinguish whether the diagnostic striae convergence is present or not.

C. laxa is a juvenile instar of *C. papilio,* as Jones and Woodward first thought (1885, p. 396). *C. murchisoni* is used to denote moderately large styles of several species, in this case of *C. papilio.* In Etheridge, Jones and Woodward's own words "*C. robusta,* being based on some small caudal appendages without carapaces, is troublesome and unsatisfactory to deal with. We find some equivalent styles and . . . stylets in *C. papilio, stygia, acuminata* etc., but none of these seem small enough for the several little sets of trifid appendages, more or less perfect, which we have met with. *C. robusta* takes in some of these; but Oxford Mus. T is relatively broad, and might be termed *lata* [= *patula* 1888]; BM 58878 from Muirkirk has very narrow members (*angusta*)." *C. longa* was first regarded as a variety of *C. robusta* (1885, p. 464) although some specimens "may well belong to *C. papilio* or *C. stygia*" (1886b, p. 458). This 'variety' was raised to species level later as the style was considered too long for either *C. papilio* or *C. stygia* (1888b, p. 43). *C. attenuata* differs in having "narrower and smaller" abdominal segments and style and stylets shorter than *C. gigas* or *C. murchisoni* (1886b, p. 456-457).

Style length is unsuitable as a character for specific differentiation since only when cameo and intaglio are available is it possible to know if the long, needle-like, distal portion of the style is preserved. Furthermore, the style is a hollow structure and appears "relatively broad" simply due to flattening during burial. It is therefore suggested that all the above mentioned 'species' belong to either *C. papilio* or *C.*

stygia, which form the subject of the present preliminary study. An account of the morphology of the species is given elsewhere (Rolfe, in press).

Although Salter (1860, p. 156) stated that *C. stygia* had its "margine ventrali plus minusve angulato," the diagnostic character of *C. papilio* was "the much shorter body — scarcely longer (tail included) than the great carapace — [which] easily distinguishes it." Jones and Woodward (1885, p. 392; 1886a, p. 341; 1888b, p. 36) misrepresented Salter's diagnosis of these two species, thus "as mentioned by Salter, one (*C. papilio*) has the carapace more oblong than the other (*C. stygia*)." This revised diagnosis led them to suggest (1885, p. 393; 1886a, pp. 341-342; 1888b, p. 36) that only the first of the three figures "termed *C. papilio*, evidently from oversight" by Salter (1860, p. 154) was in fact that species, the remaining two being *C. stygia.* Salter had already suggested (1860, p. 156) that there were "at least two varieties of carapace in *C. stygius* itself." Subsequent workers have found it difficult to distinguish the two species, and it has been suggested that they are identical (Størmer, 1935, p. 294). This difficulty was also encountered in the present study and hence the museum collections of material available to Salter and Jones and Woodward (*i.e.* their hypodigm) have been restudied to see if the species distinction could be maintained.

One complicating factor in the use of the older collections is the separation of parts from counterparts. Specimens of identical dimensions occur in different institutions, and without bringing all the material together it is impossible to be certain that part and counterpart of the same individual are not treated as two individuals. This does not affect the present study, however, since it is arguable that such duplication will be distributed evenly throughout the sample.

Two new collections have been examined to determine if, for example, *C. papilio* and *C. stygia* were allopatric or even successional species (= chrono- or palaeospecies). The first of these, the A. Ritchie collection in the Grant Institute of Geology, Edinburgh University, came from the '*Jamoytius* Beds', half a mile up the Logan Water from Logan House (Ritchie, 1960, p. 647). The other was collected by J. S. Jennings from a horizon *ca.* 700 feet higher in the succession at the locality near Logan Reservoir known as Shank's Castle (Peach and Horne, 1899, p. 573). This collection is now deposited in the Geology Department, University College of North Staffordshire.

The older material is housed in the several museums listed on Table 1. Few of the specimens have accurate localities indicated, but the majority probably came from the Shank's Castle region. Several other localities are known, however, and these have been detailed by Etheridge (1873b, p. 49). The authors wish to thank the several curators for access to collections, and Professor H. B. Whittington for reading the manuscript of this paper.

Salter's criterion for distinguishing *C. papilio* from *C. stygia* by the number of segments protruding from the carapace is artificial, since it depends solely on the degree to which the thorax and abdomen are impacted into, or drawn out from the carapace after death or exuviation. Jones and Woodward suggested that "*C. stygia* was rather larger than *C. papilio*; its telson was larger; the carapace was markedly distinct by its trapezoidal outline, deep ventral region, and mucronate antero-dorsal angle, which was not nearly so often lost in fossilization as the front angle of *C. papilio*" (1885, p. 395; 1886a, p. 344; 1888b, p. 40). Style length has already been criticised as a specific character; thus of 202 styles measured only 64 were complete and associated with the last abdominal segment. The ratio of style length/last abdominal segment length ranges from 1.5 to 2.9, and a scatter diagram of this ratio showed normal uncorrelated variation when plotted against the last abdominal segment length. This does not confirm Jones and Woodward's assertion that "in *C. stygia* the style is usually rather more than twice, and in *C. papilio* only about twice as long as the ultimate segment" (1888b, p. 39).

The remaining two characters utilised by Jones and Woodward are carapace size and shape. We here define a 'size factor' P such that

$$P = \log (LH)$$

and a 'shape factor' Q such that

$$Q = \log (L/H)$$

where L and H are the overall length and height of the carapace in millimeters. Figure 1 shows the relationship between the size and shape factors for the 128 intact carapaces listed in Table I. The distribution of points is the same as would have been obtained by plotting L against H on double-log paper and rotating the diagram through 45°. The object of performing the logarithmic transformation and rotation analytically is two-fold: to normalise the distribution of the shape factor Q, and to simplify investigation of the extent to which growth in *Ceratiocaris* is allometric.

The overall mean value of the shape factor and standard deviation were found to be

$$\bar{Q} = 0.2775 \pm 0.05917$$

corresponding to a geometric mean value of the ratio L/H of 1.894. The regression of Q on P was calculated by the first-moment method of Wald and Bartlett. The observed P values were divided into five groups and the mean values of Q and P were found for each group, the number of points in each group being 20, 20, 48, 20, and 20. The five mean points are shown on Figure 1, ($\bar{Q}_1$-$\bar{Q}_5$). Their coordinates are (2.8109, 0.3097), (3.0779, 0.2787), (3.2100, 0.2717), (3.3350, 0.2698), and (3.4830, 0.2646).

The regression is thus non-linear, although as may be seen from Figure 1, the four points $\bar{Q}_2$-$\bar{Q}_5$ lie on a practically straight line. The deviation of $\bar{Q}_1$ from this line is scarcely significant, and the line itself does not depart significantly from a direction parallel to the P axis, if the first group of points is ignored.

If we interpret the assemblage as a growth series, it follows that growth is isometric except in the range of size for which P is less than 3.07 (LH less than 1175 mm.^{2}). In this latter size range, growth is not isometric, though the degree of allometry is small and is barely significant.

Changes in the allometric constant during growth are well known in crustaceans, and commonly separate two distinct instars or mark a more critical ecdysis such as the prepuberty moult (Teissier, 1960; Simpson, Roe, and Lewontin, 1960, pp. 412-415).

If we discard the 20 smallest specimens and test the marginal distribution of the remaining 108 Q values by plotting on probability paper, we find that the distribution is an almost perfect unimodal normal curve (a straight line plot). There is thus no evidence to justify splitting up the assemblage on the basis of carapace shape. If, moreover, we regard the assemblage as a single homogeneous sample of a single species, we can readily calculate confidence limits for Q values, to test whether a given specimen may reasonably be regarded as a member of the assemblage. (It will be as well to withhold judgment in the case of very small specimens, but otherwise there should be no need to worry about allometry.)

The first writer (W.D.I.R.) has been unable to trace either of the syntypes of *C. papilio* (Salter, 1859, p. 262) and hence specimen GSM 7479, the original of Salter's 1860, p. 154, fig. 1, is here treated as the neotype of the species. Jones and Woodward accepted this specimen as a genuine *C. papilio* (= M.P.G. x $\frac{1}{15}$ in 1885, p. 393; 1886a, p. 342; 1888b, p. 36). Calcula-

TABLE I

Length (L) and height (H) of 128 museum specimens of ceratiocaridid carapaces from the Lesmahagow area, in millimeters

Specimen number	L	H
GSM-165-2	25	11
BM-24161	26	12
BM-24163	28	13
BM-59648	35	15
BM-16483	33	16
H-no number	28	19
Ke-09 123 fu	34	16
Ke-09 123 cg	42	15
Ke-Airdrie Coll.	34	19
J-LW8 R2	34	19
Ke-09 123 dy	36	18
Ke-09 123 cb	36	19
Ke-R22	37	20
GSE-6650	39	19
Ke-09 123 cd 2	41	19
BM-45161	39	20
J-27	44	18
H-Stark Coll.	45	21
BM-24150	43	23
AR 59-152	43	24
Ke-09 123 ed	48	22
GSM-X 1/13	41	26
Ke-R29	43	25
J-LW8 Q2	45	25
GSM-256	45	25
AR 59-146	49	23
BM-24151	47	24
Ke-R23	44	26
BM-41895	45	26
BM-24160	45	26
H-A1901	47	26
Ke-09 123 ex	47	26
BM-24158	50	25
AR 59-149	47	27
Ke-R8	53	24
Ke-Airdrie Coll.	48	27
E-1902/30/11	54	25
J-LW8-L	54	25
H-Macnair Coll.	54	25
H-A1902	52	26
H-66	52	26
AR 59-108	52	26
BM-16495	53	26
Ke-09 123 gb	53	26
BM-24164	52	27
H-A1908	52	27
GSM-7479	57	25
GSE-6647-1	55	26
BM-16501	52	27
K-5-3	49	30
Ke-R28	49	30
BM-24157	57	26
Ke-09 123 dn	50	30
GSM-87338	50	30
AR 59-148	54	28
E-1902/30/9	51	30
K-6-1	48	32
GSE-6647-2	57	27
H-no number	52	30
Ke-09 123 cn	60	26
K-5-2	51	31
J-LW9 E	59	27
Ke-R1	57	28
GSM-272	54	30
H-A1903	56	29
BM-no number	56	29
AR 59-154	58	28
K-5-1	52	32
H-A1904-1	49	34
AR 59-Q	60	28
BM-41896	60	28
Ke-R2	56	30
E-1902/30/7	53	32
H-A1908-3	53	32
BM-16517	57	30
Ke-09 123 dz	58	30
GSM-no number	55	32
H-A1908-2	55	32
H-T.Wise Coll.	58	31
GSM-X 1/22	60	30
Ke-09 123 ei	62	30
Ke-R3	62	30
H-A1904-2	55	34
K-8	64	30
Ke-09 123 ey	60	32
E-1902/30/4	52	37
AR 59-153	60	33
AR 59-144	60	34
AR 59-106	57	36
K-6-2	57	36
E-1902/30/10	71	29
E-1902/30/1	69	30
K-1	56	37
BM-16513	56	37
Ke-R33	62	34
AR 59-M	68	31
K-7	65	33
AR 59-P	67	32
BM-41894	64	34
J-LW8 B	59	37
H-A1900-1	58	38
Ke-R4	69	32
BM-16482-1	67	33
BM-16482-2	62	36
H-A1900-2	66	34
Ke-09 123 ez	74	33
BM-24153	67	37
AR 59-147	66	38
BM-24155	72	35
Ke-R9	78	33
AR 59-150	63	41
AR 59-151	70	38
BM-58669	83	33
Ke-R25	66	42
BM-24149	73	39
E-1891/92/6	80	36
Ke-09 123 ea	68	43
Ke-R24	70	43
BM-41898	83	37
K-3	75	41
BM-16479	82	42
GSM-X 1/21	85	46
E-1865/11/17	74	53
Ke-09 123 ce	84	47
BM-45154	90	47
GSM-X 1/19	105	50
Ke-09 123 dr	96	61
H-Macnair Coll.	100	70

Ranked according to increasing size factor P = log (LH); the five groups delineated by the heavy lines are those referred to in the text.

Repositories: AR 59 - Ritchie Collection, Grant Institute of Geology, Edinburgh University; BM - British Museum (Natural History), London; E - Royal Scottish Museum, Edinburgh; GSE - H. M. Geological Survey, Edinburgh; GSM - H. M. Geological Survey Museum, London; H - Hunterian Museum, Glasgow University; J - Jennings Collection, Geology Department, University College of North Staffordshire; K - Kilmarnock Public Museum; Ke - Kelvingrove Museum, Glasgow.

Fig. 1. Scatter diagram of the relationship between shape and size factors for carapaces of *Ceratiocaris papilio* Salter. Dots indicate 128 Lesmahagow specimens and ticks show number of individuals of identical dimensions. Crosses indicate eight specimens from the neighbouring Hagshaw Hills inlier, inserted for comparison but not included in the calculation of the five mean values $\bar{Q}_1 - \bar{Q}_5$ marked by points within triangles. Dots labelled are: GSM 7479 — suggested neotype of *C. papilio* Salter (Geological Survey Museum, London); BM 58669 — 'abnormal' specimen of *C. papilio* figured by Jones and Woodward, 1885, pl. 10, fig. 1, etc., (this and following specimens in British Museum, Natural History); BM 45154 — "*C. stygia*" figured by Jones and Woodward, 1885, pl. 10, fig. 2, etc.; BM 59648 — specimen identified as *C. inornata* by Jones and Woodward. Diagram at upper right shows outline of right carapace valve with dimensions used in defining shape and size.

tion shows that this specimen lies within the 95 percent confidence limits for group 3. The 'primary' types of *C. stygia* are unknown but one of the "good specimens of *C. stygia*" figured by Jones and Woodward (1885, pl. 10, fig. 2; 1888b, pl. 12, fig. 2) BM 45154, is similarly within the 95 percent confidence limits for group 5. *C. stygia* is thus not separable from *C. papilio* on statistical or indeed any other present evidence, and the former junior synonym should be suppressed. The morphospecies *C. papilio* and *C. stygia* form the one biospecies (or transient species) *C. papilio*. It is worth noting that the specimen of *C. papilio* figured by Jones and Woodward (1885, pl. 10, fig. 1; 1888b, pl. 12, fig. 1) BM 58669 is 'abnormal,' as can be seen from its position on Figure 1.

No significant differences in P or Q can be detected in the stratigraphically separated material of the Ritchie and Jennings collections.

There is a notable lack of clustering in terms of the size factor P corresponding to the mean size of successive moult stages or instars. Attempts to divide the Ritchie or Jennings specimens alone into instars were also unsuccessful. Intra-instar variation may obscure the limits of successive instars if sufficiently great, but not all crustaceans obey Brooks' Law (Needham, 1950, pp. 10-11), and *C. papilio* may be another exception. At least part of this difficulty is due to sampling and preservation. Thus small individuals are only rarely collected (see Fig. 1) and all large individuals found have been incomplete. Relatively gigantic specimens up to two feet in total length occur both in the Lesmahagow and Hagshaw Hills inliers, but they can only be reconstructed from fragments and hence do not appear on Figure 1. A further complicating feature of the few large specimens available is their distinctive dendritic carapace ornament. It can be argued, however, that this ornament is characteristic of adult instars (Rolfe, in press). Such giant individuals must have had younger growth stages coincident in size with the specimens of Figure 1, and no such dendritic ornament has been observed in that size range. It seems preferable to extend the name *C. papilio* to include these large individuals, at the risk of 'lumping,' until better sampling has been made.

SUMMARY

Of ten species of *Ceratiocaris* recorded from the Lesmahagow inlier, only *C. papilio* and *C. stygia* are sufficiently well founded to demand preliminary investigation. Both Salter's diagnosis of these two species and Jones and Woodward's subsequent definitions are artificial. Analysis of 128 carapaces in museum collections shows that *C. papilio* is indistinguishable from *C. stygia*, and the latter should be suppressed as a junior synonym.

Carapaces of *C. papilio* show isometric growth except in the smallest individuals. The material cannot be resolved into a series of distinct instars.

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BREVIORA

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THE GENUS BETHYLUS IN NORTH AMERICA (HYMENOPTERA: BETHYLIDAE)

BY HOWARD E. EVANS

Bethylid wasps are predominantly tropical and subtropical in distribution, with only a few species of diverse genera penetrating temperate regions and virtually none entering arctic or subarctic regions. The sole exception to this statement, illogically, is the type genus of the family, *Bethylus* Latreille. This rather highly evolved genus is circumpolar in distribution. In North America, specimens have been taken close to the Arctic Circle, but none have been taken south of New York, Illinois, Colorado, and central California. In the Old World there are several species of northerly distribution and several others from the Mediterranean region. The genus is not known from the Southern Hemisphere.

In North America, four species have been described in the genus; these are: *castaneus* Kieffer, *amoenus* Fouts, *brachypterus* Whittaker, and *flavicornis* Whittaker. A fifth species, *decipiens* Provancher, has recently been transferred to the genus by Krombein (1958, U.S. Dept. Agri., Monogr. no. 2, first suppl., p. 98). Examination of types in the U.S. National Museum reveals that two additional species, *Arysepyris californicus* Bridwell and *Perisemus oregonensis* Ashmead, properly belong in the genus. Since the latter species is the type of the genus *Digoniozus* Kieffer (1905, *In* André, Spec. Hymen. Eur. Alger., v. 9, p. 245), this name can be added to the synonymy of *Bethylus*.

One of these seven names can be removed from further consideration here. I have recently had an opportunity to study the type and only known specimen of *Bethylus castaneus* Kieffer (1907, Berlin. Ent. Zeitschr., 51: 295). The wings of this specimen are in poor condition, but enough remains to be sure that this species belongs not to *Bethylus* but to the related genus *Goniozus* (new combination).

Thus there are six specific names available for the North American *Bethylus,* three of them newly assigned to the genus. The question naturally arises as to how much synonymy is involved and how many species, in fact, are there? The present paper is an attempt to answer that question.

ANALYSIS OF THE PROBLEM

Specimens of this genus are not common in collections, but by borrowing material from many sources I was able to obtain about 80 specimens. One's first impression, on scanning this material, is the remarkable uniformity of the specimens in size, color, and structure. The only notable color differences are sexual: the males have yellow mandibles and wholly yellow antennae, while the females have dark mandibles and the antennae more or less infuscated apically. There are no noticeable differences in the structure of the mandibles and clypeus, in the sculpturing of the head or thorax, or in the male genitalia.

There is, however, one character which varies strikingly, and that is wing length. The wings vary all the way from small pads scarcely larger than the tegulae to wings of normal size. This is not unusual in the genus, as several brachypterous species have been described and the European *fuscicornis* is known to exhibit much variation in wing length. In the case of the North American *Bethylus,* it was of interest to know whether wing length varied in a continuous spectrum or whether there were certain wing-length types which might represent different species. Following O. W. Richards (1939, Trans. R. Ent. Soc. London, 89: 185-344) in his revision of the British species, I first determined the relative wing length of each specimen by dividing the length of the fore wing by the length of the hind tibia (which is much easier to measure accurately than total body length). I then plotted the number of individuals exhibiting a given relative wing length (Fig. 1). The males fell into two distinct groups. Those of the first group (Type A) might be termed subapterous, since the wings are exceedingly small, barely surpassing the anterior margin of the propodeum. Males of the second group (Type B) might be termed micropterous, since the wings are still very small, extending about to the beginning of the propodeal declivity. When one plots the females on this same scale he obtains a somewhat different picture (lower half of Fig. 1). The subapterous forms (Type A) tend to have slightly longer wings, the micropterous forms (Type B) slightly shorter wings,

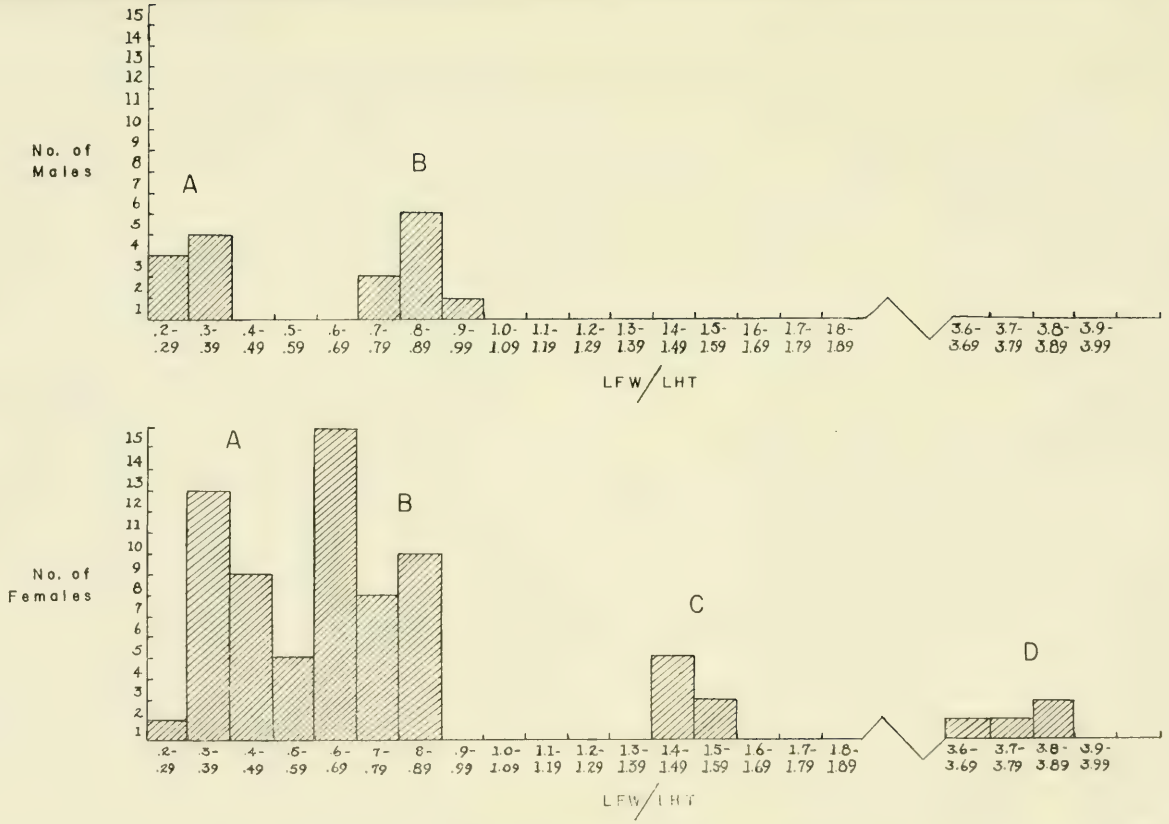

Fig. 1. Numbers of individuals (ordinate) exhibiting given relative wing lengths (length of fore wing [LFW] divided by length of hind tibia [LHT]), males at top, females at bottom.

so that the two curves overlap slightly. Furthermore, there is a class of individuals with wings of moderate length, reaching about to the posterior margin of the first abdominal tergite, which might be termed brachypterous (Type C), as well as a few individuals with wings of normal length (macropterous, Type D).

The fact that wing length varies discontinuously suggests the possibility that several species may be involved, each exhibiting a different wing length. Presumably there would be four such species, with males of the two less common ones still to be discovered. However, in the absence of other characters one cannot rule out the possibility of polymorphism.

I once again turned to Richards' study of the British species, and discovered that the most useful character for separating the three forms occurring in Britain is the ratio between the distance separating the hind ocelli and the distance separating the hind ocelli from the occiput. I determined this ratio for all specimens available to me but obtained a unimodal curve, with the mean 1.7, the range of variation from 1.3 to 2.2 (close to the range for the European *fuscicornis*). Thus these measurements failed to support the possibility of more than one species. However, in the course of making the measurements I found myself able to recognize "long-headed" and "short-headed" individuals. The difference was slight, but sufficient to induce me to measure the heads and determine the width/length ratio. In the case of the males I again obtained two separate curves (Fig. 2, top). For the females I obtained a bimodal curve (Fig. 2, bottom). It was at once apparent that all the subapterous individuals (Type A) were "long-headed" (left hand curves in Fig. 2), all the micropterous individuals (Type B) "short-headed" (right hand curves in Fig. 2). The brachypterous females (Type C) were all "short-headed", while the fully winged females (Type D) were of both types.

Here was a suggestion that two species might be involved, with both species being polymorphic for wing length in the female sex. Upon sorting the specimens into two lots representing probable species, several other differences previously overlooked or discounted in importance were discovered. The most important of these involved the sculpture of the propodeum, the shape of the male subgenital plate (Fig. 3), and the wing venation of the few available fully winged females. Thus I am now convinced that two polymorphic species are involved. The name *amocnus* Fouts is applicable to the "long-headed" species, while

decipiens (Provancher) is the earliest name for the "short-headed" species. The two species are widely sympatric east of the Rockies, but *amoenus* is not known to occur west of the Rockies. The characters separating the two species are summarized below, as are their synonymy and distribution.

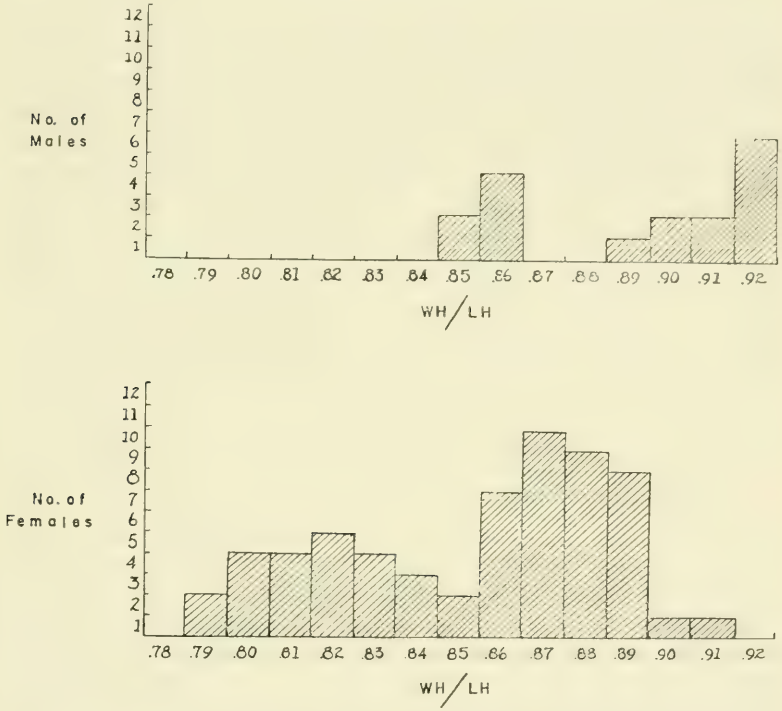

Fig. 2. Numbers of individuals (ordinate) exhibiting given relative head lengths (width of head [WH] divided by length of head [LH]), males at top, females at bottom.

The only good series of *decipiens* from one locality is the series of 16 females and 4 males from Chilliwack, British Columbia, on which Whittaker based his descriptions of *brachypterus* and *flavicornis*. As discussed further below, I have studied or obtained the necessary information on this entire series. Twelve of the females are micropterous (Type B), three are brachypterous (Type C), and one is macropterous (Type D). This 12:3:1 ratio, obtained in a series from one locality, is approached rather closely by the ratio for the species throughout its range,

which is 41:9:4. Unfortunately, only one reared series of this species is available. That is a series of five females and three males in the U.S. National Museum reared from *Vicia angustifolia* at the Lummi Indian Reservation, Washington. All individuals in this series are micropterous.

Unfortunately, no good series of *amoenus* is available; the longest series consists of three females and a male taken on different dates at Bar Harbor, Maine. All of these individuals are subapterous, and in fact only one fully winged individual of this species is known. This is a female taken by O. W. Richards on the window of an automobile at Buffalo, N. Y., 19 Sept. 1928. The ratio of subaptery: brachyptery: macroptery in the females of this species is 23:0:1. It is, of course, entirely possible that brachypterous individuals of *amoenus* may some day be discovered. It is also quite possible that polymorphism for wing length may occur in the male sex. At present only seven males of *amoenus* are known, only thirteen of *decipiens*. Clearly any hypotheses on the genetics of polymorphism in these wasps will have to await the day when much more material has accumulated in museums. At present it appears that only the females are polymorphic for wing length and that the polymorphism arises from a very simple genetic mechanism.

The Nearctic *decipiens* is undoubtedly closely related to the Palaearctic *fuscicornis* and may well be derived from it. Not only are the ocellar measurements similar, as noted earlier, but the sculpturing of the propodeum is similar and the male subgenital plate virtually identical. However, there is no doubt in my mind that they are specifically distinct. The antennae of *fuscicornis* are shorter and the scape is black at the base, yellowish apically (the scape is wholly yellowish-brown in both Nearctic species). Richards has found that the frequency distribution of relative wing length in *fuscicornis* is more or less trimodal or quadrimodal, but less distinctly so than in *decipiens* and with a much larger proportion of longer-winged individuals. Furthermore, the males of *fuscicornis* are typically macropterous rather than micropterous as in *decipiens*.

TAXONOMIC TREATMENT

Key to North American Species of Bethylus

Propodeum with a median polished ridge, remainder of disc contrastingly alutaceous; head rather short (width/length ratio

.85-.91 in female, .89-.92 in male); wings of micropterous individuals reaching at least nearly to middle of propodeal disc (relative wing length .57-.91); fully winged individuals with radial vein curved upward sharply apically, vein arising from basal vein barely indicated; fore tibiae clear yellow; male subgenital plate strongly emarginate, but the side-pieces relatively broad and blunt (Fig. 3, a) . . *decipiens* (Provancher)

Propodeum somewhat convex dorsally but without a median ridge which is set off from the remainder of the disc; head slightly longer (width/length ratio .79-.84 in female, .85-.86 in male); wings of most individuals extremely small, reaching barely beyond anterior margin of propodeum (relative wing length .26-.54); fully winged individuals with radial vein not curved upward sharply at apex, vein arising from basal vein nearly as long as transverse median vein; fore tibiae of female usually at least weakly suffused with brownish; male subgenital plate with a strong emargination, the side-pieces reduced to slender, acuminate processes (Fig. 3, b) . . . . . *amoenus* Fouts

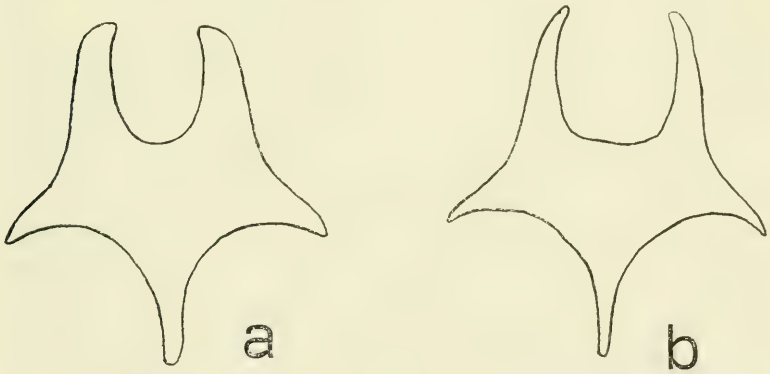

Fig. 3. Subgenital plates of (a) *Bethylus decipiens* and (b) *Bethylus amoenus*.

BETHYLUS DECIPIENS (Provancher)

Gonatopus decipiens Provancher, 1887, Add. Corr. Faune Ent. Canada, Hymen., p. 179 [Type: ♀, Cap Rouge, Quebec (Que. Prov. Mus., yellow label no. 1332)]. — Muesebeck and Walkley, 1951, U. S. Dept. Agri. Monogr. 2, p. 1038.

Perisemus oregonensis Ashmead, 1893, Bull. U. S. Nat. Mus., 45: 70 [Type: ♀, Portland, Oregon (U. S. Nat. Mus. no. 40422)]. New synonymy.

Digoniozus oregonensis Kieffer, 1905, Spec. Hymen. Eur. Alger., 9: 245 [Made type of new genus *Digoniozus*]. — Muesebeck and Walkley, 1951, U. S. Dept. Agri. Monogr. 2, p. 732.

Arysepyris californicus Bridwell, 1919, Proc. Hawaiian Ent. Soc., 4: 34 [Type: ♀, Parkside, San Francisco Co., Calif. (U. S. Nat. Mus. no. 64124)]. New synonymy.

Bethylus brachypterus Whittaker, 1929, Trans. R. Ent. Soc. London, 76: 385 [Type: ♀ (not ♂ as stated), Chilliwack, Br. Col. (British Museum)]. — Muesebeck and Walkley, 1951, U. S. Dept. Agri. Monogr. 2, p. 732. New synonymy.

Bethylus flavicornis Whittaker, 1929, Trans. R. Ent. Soc. London, 76: 386 [Type: ♂, Chilliwack, Br. Col. (British Museum)]. — Muesebeck and Walkley, 1951, U. S. Dept. Agri. Monogr. 2, p. 732. New synonymy.

Glenosema californicus Muesebeck and Walkley, 1951, U. S. Dept. Agri. Monogr. 2, p. 727.

Bethylus decipiens Krombein, 1958, U. S. Dept. Agri. Monogr. 2, First Suppl., p. 98.

Remarks on types. — Provancher's *decipiens* was transferred to *Bethylus* by Krombein upon his examination of the type. Dr. Krombein has kindly placed his notes at my disposal, and they leave no doubt that Provancher's name applies to this species. The propodeum is alutaceous but with a median polished ridge, and the wings extend almost to the posterior slope of the propodeum. The type is in good condition.

The type of Ashmead's *oregonensis* is also in good condition and is a fully winged female of this species. The type of Bridwell's *californicus* is unfortunately in poor condition, the head, abdomen, and legs all being missing. However, the wings and propodeum are typical of the micropterous form of *decipiens*. A topotypic female in the collection of the California Academy of Sciences is very similar to the type and is in good condition.

Whittaker's two names require special discussion. The types and most of the paratypes are in the British Museum and I have not seen them. However, Mr. G. E. J. Nixon has been good enough to examine these specimens and send me the critical information on them. I have studied one paratype of *brachypterus* in the collection of Cornell University as well as two of this species and one of *flavicornis* in the collection of Robert M. Fouts of Laredo, Texas. The characters Whittaker used for separating the two species are color characters which happen to be those which separate the sexes, and it happens that all the specimens

of *brachypterus* are females and all of *flavicornis* are males — Whittaker's statements to the contrary notwithstanding. The entire series is from Chilliwack, British Columbia; the type of *brachypterus* is a fully winged female, that of *flavicornis* a micropterous male. As indicated earlier, three of the paratypes of *brachypterus* are brachypterous, the remaining twelve micropterous.

Specimens examined. — 40 ♀♀, 10 ♂♂. ALASKA: 1 ♀, Fairbanks, 25 June 1948 [USNM]; 1 ♀, Circle, 2 July 1958 (C. Lindroth) [CNC]; 1 ♀, Nenana, 17 June 1953 (R. I. Sailer) [USNM]; 1 ♀, 2 ♂♂, Mile 1476, Alaska Highway (C. Lindroth) [CNC]. BRITISH COLUMBIA: 1 ♀, Mile 290, Alaska Highway, 19 June 1951 (W. Mason) [CNC]; 1 ♀, Smithers, 12 June 1958 (C. Lindroth) [CNC]; 1 ♀, Cranbrook, 12 May 1922 (C. Garrett) [CNC]; 1 ♀, Victoria, 28 Aug. 1923 (K. F. Auden) [CNC]; 3 ♀♀, 1 ♂, Chilliwack, May-June, Sept. 1927 (O. Whittaker) [CU, Coll. R. M. Fouts]; 1 ♂, Galiano, 2 Aug. 1929 [Coll. Fouts]; 1 ♀, Kaslo (A. N. Caudell) [USNM]; 2 ♀♀, Terrace [MCZ]. WASHINGTON: 1 ♀, Olympia [USNM]; 5 ♀♀, 4 ♂♂, Red River Rd., Lummi Ind. Res., 1 Aug. 1944 (*Vicia angustifolia*, W. W. Baker) [USNM]. OREGON: 1 ♀, Portland [USNM]; 1 ♀, Forest Grove, 1 Apr. 1919 (A. C. Burrill) [USNM]; 1 ♀, Ashland Loop, Siskiyou Mts., Jackson Co., 6 Aug. 1950 (Malkin & Thatcher) [CAS]. CALIFORNIA: 1 ♀, Land's End, San Francisco, 11 July 1922 (F. X. Williams) [CAS]; 1 ♀, Parkside, San Francisco Co., 8 Sept. 1910 (J. C. Bridwell) [USNM]. UTAH: 1 ♀, Logan [MCZ]. COLORADO: 2 ♀♀, 1 ♂, Fort Collins, June, Sept. 1895 (C. F. Baker) [USNM]. IDAHO: 1 ♀, Coeur d'Alene (H. J. Rust) [USNM]. ALBERTA: 1 ♀, Edmonton, June 1917 [USNM]; 1 ♂, Elkwater Lake, 19 July 1956 (O. Peck) [CNC]. ONTARIO: 1 ♀, Sudbury, 1892 [CNC]. QUEBEC: 1 ♀, Anticosti Island, 9 Sept. [MCZ]. NEW BRUNSWICK: 1 ♀, Penobsquis, Dec. 1927 (C. A. Frost) [MCZ]. NOVA SCOTIA: 1 ♀, Portapique, 23 July 1929 (C. A. Frost) [MCZ]. MAINE: 4 ♀♀, Bar Harbor, July-Oct. (A. E. Brower) [USNM]. NEW YORK: 1 ♀, Grand Island, 11 Oct 1922 [USNM]; 1 ♀, North Fairhaven, 1 Sept. 1918 [CU].[1]

[1] The following abbreviations have been employed for the museums involved: CAS, California Academy of Sciences, San Francisco; CNC, Canadian National Collections, Ottawa; CU, Cornell University, Ithaca; MCZ, Museum of Comparative Zoology, Cambridge; USNM, U. S. National Museum, Washington.

Map showing distribution of North American *Bethylus*. Solid triangles: *Bethylus amoenus,* subapterous form; hollow triangle: macropterous form of *amoenus*. Solid circles: *B. decipiens,* micropterous form; half-solid circles: brachypterous form of *decipiens;* hollow circles: macropterous form of *decipiens*.

Bethylus amoenus Fouts

Bethylus amoenus Fouts, 1928, Proc. Ent. Soc. Wash., 30: 127 [Type: ♀, Slaterville-Caroline, Tompkins Co., N.Y., 14 June 1904 (Cornell Univ. no. 934)]. — Muesebeck and Walkley, 1951, U. S. Dept. Agri. Monogr. 2, p. 732.

Remarks on types. — The type is in good condition. I have also studied a male allotype, bearing the same data, in the collection of Robert M. Fouts.

Specimens examined. — 24 ♀♀, 7 ♂♂. NORTHWEST TERRITORIES: 2 ♀♀, Norman Wells, 3-13 July 1949 (W. Mason) [CNC]. ALBERTA: 1 ♀, Aspen Beach, 23 Aug. 1944 (O. Peck) [CNC]; 1 ♀, Elkwater Lake, 19 July 1956 (O. Peck) [CNC]. SASKATCHEWAN: 1 ♂, White Fox, 10 July 1944 (O. Peck) [CNC]; 1 ♂, Holdfast, June 1946 (W. A. Nelson) [CNC]; 1 ♀,

Assiniboia, June 1955 (J. R. Vockeroth) [CNC]; 1 ♂, Saskatoon, 15 Sept. 1924 (K. M. King) [CNC]. MINNESOTA: 1 ♀, Eaglesnest, 26 Aug. 1959 (W. V. Balduf) [USNM]. WISCONSIN: 1 ♀, Cranmoor, 20 May 1910 (C. W. Hooker) [USNM]. ILLINOIS: 1 ♀, Palos Park, 17 March 1933 (Frison & Mohr) [Ill. Nat. Hist. Survey]. MICHIGAN: 1 ♀, Wexford Co., 4 July 1952 (R. R. Dreisbach) [Coll. Dreisbach]; 1 ♀, Presque Isle Co., 28 July 1952 (P. B. Kannowski) [Coll. Dreisbach]; 1 ♀, Midland Co., 20 June 1945 (R. R. Dreisbach) [Coll. Dreisbach]. ONTARIO: 1 ♀, Jordan, 25 Sept. 1916 (W. A. Ross) [CNC]: 1 ♀, Rondeau Park, Kent Co., 28 June 1936 (G. Steyskal) [Coll. Dreisbach]; 1 ♀, Prince Edward Co., 10 July 1950 (J. F. Brimley) [CNC]; 1 ♀, Belleville, 2 Oct. 1956 (J. M. Smith) [CNC]. NEW YORK: 1 ♀, Buffalo, 19 Aug. 1928 (O. W. Richards) [MCZ]; 2 ♀♀, Ithaca, 28 May, 23 June (Babiy, Evans) [CU, MCZ]; 1 ♀, 1 ♂, Slaterville-Caroline, 14 June 1904 [CU, Coll. R. M. Fouts]; 1 ♂, Caroline-Harford, Tompkins Co., 15 June 1904 [CU]; 1 ♂, Gannett Hill, 30 Aug. 1925, 2000 feet [CU]. MAINE: 3 ♀♀, 1 ♂, Bar Harbor, July, Sept., Oct. (A. E. Brower) [USNM]; 1 ♀, Southwest Harbor, 6 Sept. 1922 [CU]. NOVA SCOTIA: 1 ♀, Portapique, 22 July 1929 (C. A. Frost) [MCZ].

BIOLOGY OF THE GENUS

The only specimen of this genus which I have collected was taken walking over the ground in a small sand pit. Several specimens in collections are labeled as having been taken sweeping, one while "sweeping Carex," another "while beating for ants." Several specimens of both species were taken by A. E. Brower at Bar Harbor, Maine, on "Great Heath," one of the female *decipiens* "on flowers of *Ilex verticillata*." A female *amoenus* from Palos Park, Illinois, is labeled "in wet peat sample," while a series of *decipiens* from the Lummi Indian Reservation, Washington, is labeled "Rd *Vicia angustifolia*." Apparently these insects occur in a variety of situations. *B. amoenus* has been collected in every month from March to October, *decipiens* from April to October and also in December.

Two specimens of *amoenus* bear host data. One is the female listed above from Cranmoor, Wisconsin, which is indicated as a probable parasite of *Eudemis vacciniana*. This name is now regarded as a synonym of *Rhopobata naevana* (Hbn.), an oleuthreutid moth known as the black-headed fireworm. The other

specimen is the female listed from Belleville, Ontario, which is labeled as a parasite of *Brachypterolus pulicarius* L. This is a nitidulid beetle introduced from Europe to the United States about 1918.

If the latter record is correct, it is the only known instance of a *Bethylus* attacking a beetle. The European *cephalotes* Förster and *fuscicornis* (Jurine) attack various caterpillars, chiefly Microlepidoptera but occasionally Noctuidae. The female wasps sting and malaxate their rather large prey, then drag it to a place of concealment, such as a hollow stem. Several eggs are laid on the prey and several larvae develop on a single host. Further details regarding the biology of these two species may be found in the papers of Richards (1932, Trans. Ent. Soc. So. England, 8: 35-40; 1939, Trans. R. Ent. Soc. London, 89: 185-344).

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. JANUARY 12, 1962 NUMBER 151

A NEW PHYLLOCARID CRUSTACEAN FROM THE UPPER DEVONIAN OF OHIO

BY W. D. IAN ROLFE

INTRODUCTION

When curating the collections of non-trilobite arthropods in the Museum of Comparative Zoology, the writer recently found a fossil crustacean which had been sent to Professor P. E. Raymond for determination. The specimen was received from the Cleveland Museum of Natural History through Dr. D. H. Dunkle in January 1944; the late Professor Raymond published no description of the specimen and left no manuscript notes with it. Recent collecting in the same area by Mr. G. Lammers of the Cleveland Museum failed to find further specimens, although a fragment of a second specimen from a different locality was recently donated to the Museum of Comparative Zoology by Mr. R. Pritschau of Cleveland. This specimen will be referred to as the MCZ specimen to distinguish it from the original Cleveland Museum specimen.

During the preparation of this description Mr. Lammers called the writer's attention to the fact that H. K. Brooks of the University of Florida had collected and studied the echinocaridids of this region. In correspondence, Mr. Brooks informed the writer that he had photographed this specimen some years ago, but was kind enough to allow the writer to submit this account for publication.

The writer is indebted to Dr. G. A. Cooper, Professor A. La Rocque and Professor F. G. Stehli for searching through the collections at the U. S. National Museum, the Ohio State University and Western Reserve University, Cleveland, for additional material, and to Mr. W. E. Scheele, Director of the Cleveland Museum of Natural History, for allowing the specimen to be retained for description. Professor H. B. Whittington kindly took the photograph for Plate 1 and offered helpful criticism of the manuscript.

SYSTEMATIC DESCRIPTION

Subclass MALACOSTRACA Latreille, 1806

Superorder PHYLLOCARIDA Packard, 1879

Order ARCHAEOSTRACA Claus, 1888

Suborder RHINOCARINA Clarke *in* Zittel-Eastman, 1900

Family OHIOCARIDIDAE fam. nov.

Diagnosis. Carapace valves deep, with anterodorsal-medioventral fold and broad median dorsal plate. Rostral plate and number of thoracic and abdominal segments unknown.

Remarks. The family Rhinocaridiidae comprises five genera which form a compact group characterised by elongate carapace valves and a narrow median dorsal plate. The present genus is so distinct from the previously described Rhinocarina as to warrant the erection of a second family.

Genus OHIOCARIS gen. nov.

Type species. Ohiocaris wycoffi sp. nov.

Diagnosis. As for the family.

OHIOCARIS WYCOFFI sp. nov.

Plate 1; Figure 1

Description. The Cleveland specimen is exposed with the dorsal surface of the carapace uppermost in one half of a concretion. It is preserved as a very thin film of golden brown ?cuticular material, but this has been destroyed over much of the specimen so that an internal mould is revealed. The concretion has been split apart so that the two carapace valves and median dorsal plate are separated by matrix from two complete abdominal segments, a fragment of a third, and stylet fragments. The whereabouts of the counterpart of the concretion are unknown.

As may be seen from Figure 1 and Plate 1, the carapace valves are deep; a well-defined fold, semicircular in cross section, runs from the anterodorsal region of each carapace valve, immediately posterior of the strong carapace horn, and dies out ventrad of the centre of the valve. The ventral or free margin of each valve is bordered by a narrow reflexed rim except in the midventral region, where it continues as a marginal ridge inside the ventral margin.

The broad median dorsal plate is separated anteriorly from the cephalic region of the carapace by a shallow transverse groove. The grooves laterally separating the plate from the main area of the carapace valves are narrower and deeper than the anterior groove, and are confluent posteriorly with the carapace

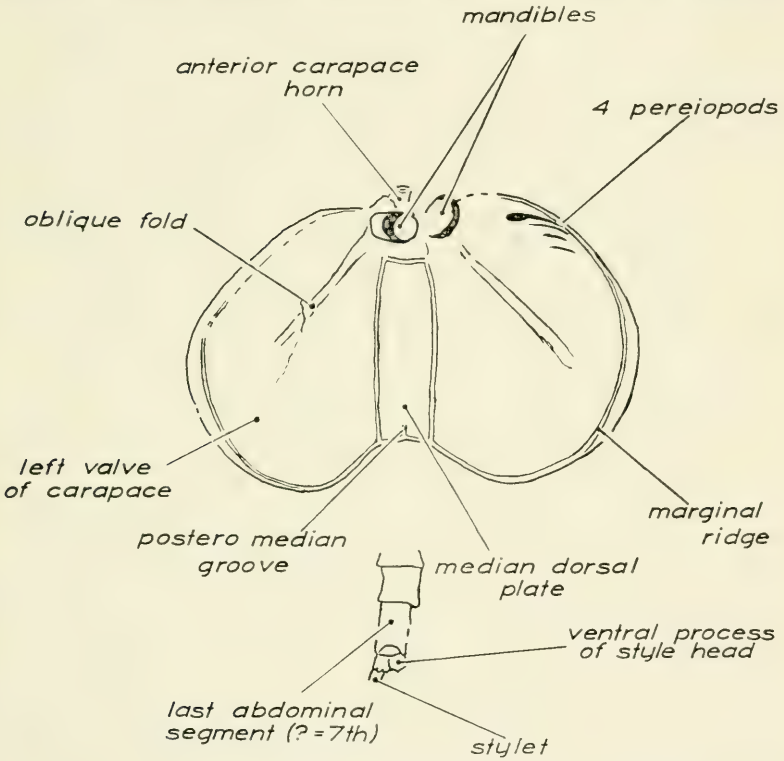

Figure 1. Outline drawing of *Ohiocaris wycoffi* gen. et sp. nov. showing structures visible on Plate 1. Cleveland Museum of Natural History 33241. x 1.1.

rim and a groove marking the posterior edge of the median dorsal plate. These grooves doubtless mark the position of marginal rims analogous in structure to those at the ventral edge of the carapace valves. The plate bears a faint posteromedian groove which extends anteriorly for 1.4 mm.

The carapace valves and median dorsal plate are crazed by

veinlets of a brown mineral (?collophane), whereas the abdominal segments and the matrix are unaffected, indicating differential chemical desiccation. The fragments of test preserved are smooth and free from ornament and the few wrinkles present are clearly secondary.

The abdominal segments are inverted relative to the carapace and thus the style and stylets are exposed ventral side uppermost. The last segment (?7th) is 1.3 times the length of the preceding segment and has a concave posteroventral margin. After the photograph for Plate 1 was taken, the fragmentary style and stylets were broken from the matrix. The dorsal head of the style thus exposed was found to be of the echinocaridid type illustrated by *Echinocaris sublevis* Whitfield, 1880, figure 6 (=Hall and Clarke, 1888, pl. 29, fig. 13). Only the bases of style and stylets are preserved but the former is triangular in cross section and much shorter than the stylets. As in all the known archaeostracans, the head of the style embraces the proximal portions of the stylets laterally and ventrally. A small denticle, 0.2 mm. long by 0.4 mm. broad, projects posterolaterally from the right lateral edge of the ventral style process or platform.

The cuticle of the style head, stylets and abdominal segments lacks ornament.

Only the inflated coxal parts of the mandibles are preserved, and excavation has failed to reveal the toothed gnathal lobes which were probably broken off at burial. The mandibles have been impressed through the anterodorsal region of the carapace valves, and the plane of section shows the left mandible to have had a wall thickness of 0.7 mm.

At least four recurved ridges on the anteroventral region of the carapace fairly certainly mark the position of simple pereiopods. As they are only seen as impressions through the thin cuticle of the carapace no detail of their structure can be discerned.

The MCZ specimen is a fragment showing the median dorsal plate only.

Dimensions, in millimeters

Cleveland Museum of Natural History 33241	
Maximum length of undistorted right carapace valve	34.0
Maximum height of undistorted right carapace valve, to right edge of groove bordering median dorsal plate	25.0

Length of median dorsal plate, along mid-line	21.0
Maximum width of median dorsal plate, at a point 7 mm. posterior from transverse groove	7.3
Length of penultimate abdominal segment	4.3
Length of last abdominal segment	5.5
Maximum dorsal width of style head	4.5
Length of style head to base of style	3.3
Width of style at base	1.1
Cross-sectional diameter of stylet	1.6
Museum of Comparative Zoology 6556	
Maximum length of median dorsal plate	*ca.* 21
Maximum width of median dorsal plate	7.2

Holotype. Cleveland Museum of Natural History 33241. Collected by Dale Wycoff, 25th May, 1934, from the Chagrin Shale, Upper Devonian. Locality — shore of Lake Erie at mouth of Porter Creek, 12 miles west of Cleveland, Cuyahoga County, Ohio.

Other material. Museum of Comparative Zoology 6556. Collected by Raymond Pritschan and donated to the Museum via G. Lammers, July 31, 1961; found as float from Chagrin Shale. Locality — Painesville, 25 miles northeast of Cleveland, Lake County, Ohio (? Whitfield's 1880, p. 37, Leroy locality).

Remarks. The spread out carapace valves of the Cleveland specimen recall the condition in *Dithyrocaris,* which possibly lived with the valves in this attitude. The marginal rim foreshadows the well-developed submarginal wall and doublure structure of *Dithyrocaris,* and is similar to the condition in the ceratiocaridids *Caryocaris curvilata* (Gurley) and *Callizoe bohemica* Barrande. The anterodorsal-medioventral fold is more anteriorly situated than that of *Pephricaris horripilata* Clarke, whereas the "Schrägrippe" and "Schnabelfurche" of *Silesicaris nasuta* Gürich (1929, p. 29) run closer to the ventral margin. As mentioned above, the style resembles that in *Echinocaris* rather than that in any rhinocaridid, but the long smooth last abdominal segment is different from that of every species of that genus.

The posteromedian groove on the median dorsal plate may prove to be of phylogenetic significance as a vestige of the non-rhinocaridid simple dorsal hinge, and homologous with the median fold of other members of the Rhinocarina. *Ohiocaris* shows the greatest development of the median dorsal plate and suggests a derivation from the Middle and early Upper Devonian rhinocaridids. Thus the plate width/carapace width ratio is 0.146 in

Ohiocaris, but only 0.096 in the specimen of *Elymocaris siliqua* figured by Beecher (1902, pl. 19, fig. 8; Yale Peabody Museum 22410). Hall and Clarke's reconstruction of *Mesothyra oceani* (1888, pl. 32, fig. 1) is inaccurate in showing the hypothetical median dorsal plate too broad. Measurement of the specimen upon which this reconstruction was based (New York State Museum 4576) shows that the ratio is 0.073, not 0.150 as figured. Two other specimens of *M. oceani* (NYSM 4577, 4581) give comparable ratios of 0.093 and 0.082, and in the *Rhinocaris columbina* figured by Clarke (1893, fig. 4, NYSM 4786) the ratio is only 0.074.

The concretion in which the Cleveland specimen occurs has the characteristic orange colour of oxidised Chagrin material described by Cushing, Leverett and Van Horn (1931, p. 34). Fossils do not seem to have been recorded previously from the Chagrin west of Cleveland (Cushing *et al.*, 1931, p. 35). The MCZ specimen forms part of a small collection comprising many of the same species of brachiopods and pelecypods as those listed by Cushing *et al.* (1931, p. 35), and in addition the crustaceans *Echinocaris multinodosa* Whitfield, *E. sublevis* Whitf. and *Palaeopalaemon newberryi* Whitf..

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Plate 1. *Ohiocaris wycoffi* gen. et sp. nov., Cleveland Museum of Natural History 33241, x 1.7.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS. JANUARY 15, 1962 NUMBER 152

NEW AUSTRALIAN DACETINE ANTS OF THE GENERA *MESOSTRUMA* BROWN AND *CODIOMYRMEX* WHEELER (Hymenoptera — Formicidae)

BY ROBERT W. TAYLOR

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The two new species described below are of considerable interest as members of the Australian ant fauna. The rare genus *Mesostruma*, to which *Mesostruma browni* n. sp. is added, includes two previously described species which have recently been revised by W. L. Brown, Jr. (1952). *Mesostruma* is known only from eastern Australia and occupies an important phylogenetic position in the subtribe Epopostrumiti, being almost exactly intermediate in character between the major Australian genera *Epopostruma* Forel and *Colobostruma* Wheeler. *Codiomyrmex flagellatus* n. sp. is the second member of its genus to be described from northern Queensland, and as such is the second representative of the important short-mandibulate stock of the subtribe Strumigeniti to be recorded from Australia. The deficiency of this element in the Australian fauna is of considerable zoogeographic interest. Its historical absence or scarcity on the continent has perhaps been important in allowing adaptive radiation of the short-mandibulate Epopostrumiti of the genus *Colobostruma* (Brown, 1952, 1959; Brown and Wilson, 1959).

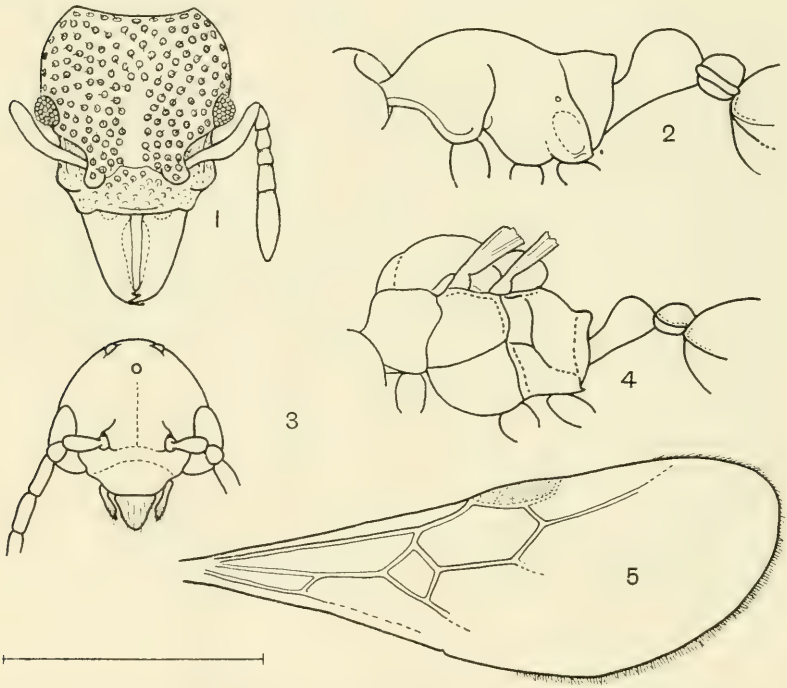
MESOSTRUMA BROWNI new species

(Figs. 1-5)

Holotype worker. Synthetic aggregate length (TL)[1] 3.6; head length (HL) 0.78; head width (HW) 0.71; mandibular extension (ML) 0.37; Weber's length of alitrunk (WL) 0.84; cephalic

[1] All measurements stated in the present paper are given in millimeters, with indices in units. The conventions followed in measurements are those established for the Dacetini by Brown (1953a, 1953b). An ocular scale with units of 0.0168 mm. was used for measuring, with correction to the nearest unit, the maximum error being estimated as ±0.01 mm.

index (CI) 91; mandibulo-cephalic index (MI) 47. Corresponding precisely with the generic characteristics cited by Brown (1948, 1952) for head shape, mandibular and antennal structure, petiole and postpetiole form, and body sculpturing. Head shape as in Figure 1, similar to large *M. laevigata* workers, but clypeus and anterior part of head somewhat more transverse. Eyes small, strongly convex as in *M. turneri*. Humeral angles rounded; dorsum of alitrunk in profile strongly and evenly convex. Propodeal lamellae as in Figure 2, more extensive than in either previously described species. Petiolar node as in Figure 2, similar to that of *M. turneri*, but more massive and less acute above in side view.



Mesostruma browni new species, Figs. 1 and 2, worker (Holotype). Fig. 1. Full-face view of head. Fig. 2. Alitrunk, nodes and base of gaster in side view. Figs. 3-5, male (Allotype). Fig. 3. Full-face view of head. Fig. 4. Alitrunk, nodes and base of gaster in side view. Fig. 5. Forewing. Pilosity and sculpture omitted from Figs. 2-4. Scale line: 1 mm.

Sculpture of head, alitrunk and petiole consisting of large circular umbilicate foveae, more widely spaced than in the other described species, rarely separated by distances less than their maximum diameter; the surfaces between them smooth and strongly shining. Dorsum of alitrunk less densely sculptured than head, with a median longitudinal area almost devoid of foveae. Posterior parts of sides of alitrunk opaque, the foveae indistinct and mixed with coarse punctures. Foveae of petiolar node smaller than those of head and alitrunk; those of postpetiole indistinct, postpetiolar dorsum finely and irregularly sculptured and feebly shining. Dorsum of first gastric segment smooth and strongly shining, with no trace of longitudinal striae.

Color rich golden brown; petiole, base and apex of gaster, legs, mandibles and antennae lighter.

Type locality. Two miles east of Berry, New South Wales (B. B. Lowery).

Worker variation. Thirty-two *paranidotype workers,* collected with the holotype, have the following dimensions: TL 3.2-3.9; HL 0.72-0.83 (mean 0.77); HW 0.66-0.74 (mean 0.71); ML 0.32-0.38 (mean 0.35); WL 0.77-0.92; CI 89-96; MI 42-49. No significant structural variation is indicated in the series. The workers are monomorphic with no bimodality in the frequency distributions of the dimensions listed, and no perceptible allometric differentiation between the head and mandibular dimensions, within the sample.

The measurements and indices of ten paratype specimens from Riverview College, Sydney (B. B. Lowery), fall within the above ranges and have almost identical means, but an eleventh specimen of the same series is much smaller: TL 3.1; HL 0.69; HW 0.62; ML 0.34; WL 0.74; CI 90; MI 49. The HL of this individual is 2.80 standard deviation units smaller than the overall mean HL of all 45 specimens examined (76.7 ± SD 2.75), its HW is 3.0 standard deviation units smaller than the overall mean HW (70.4 ± SD 2.80). The specimen is thus of extremely small size when compared with workers from mature colonies, and is perhaps an old nanitic which had survived into the mature colony with which it was collected.

A single paratype worker from Barrington Tops, New South Wales (T. E. Woodward), has the following dimensions: TL 3.2; HL 0.72; HW 0.66; ML 0.32; WL 0.77; CI 92; MI 44.

Paratype queens. The first series of dimensions are those of an alate from Burns Bay, Sydney (B. B. Lowery); the second

series those of a dealate from Pymble, New South Wales (C. Mercovich). TL 4.0, 4.3; HL 0.80, 0.86; HW 0.76, 0.82; ML 0.37, 0.40; WL 1.07, 1.16; CI 95, 95; MI 46, 46. Differing from the workers in the usual characters of full sexuality: larger size, presence of ocelli and wings, and unreduced structure of alitrunk. Coloration as in worker, the ocellar area dark brown. Wings clear with pale yellow veins, venational pattern similar to male. The same diagnostic features as those of the worker serve to distinguish queens from those of *M. turneri*.

Allotype male. TL 3.0; HL 0.54; HW including compound eyes 0.63; WL 0.88; forewing length *ca.* 2.2 mm. Head as in Figure 3. Compound eyes large, elliptical, strongly convex, their longest diameters about 0.28 mm. Mandibles slender, acute, probably not opposable. Antennae robust, thirteen segmented. Maxillary and labial palpi well developed; palpal formula apparently maxillary 5, labial 3, as in the worker (the mouthparts have not been dissected from the unique specimen). Body profile as in Figure 4. Mesonotum with well developed notauli, their posterior portion, forming the stem of the "Y," indistinct. Propodeal lamellae smaller than in the female castes. Petiole sub-clavate, the node low, sloping gradually back from the anterior peduncle; antero-ventral tooth obsolete. Lateral edges of post-petiole lacking aliform appendages, but each with a distinct, low, obtuse, longitudinal carina. Gaster broad, somewhat flattened basally; the basal edges of its first segment feebly carinate longitudinally, as in many epopostrumite workers. Genitalia exposed, enfolded by the parameres. The latter similar to those of *Orectognathus* (Brown, 1953b): broad in dorsal view, with convex lateral outlines and strongly concave inner faces, the apices rounded with their tips turned inwards and opposed mesally. Apex of sub-genital plate acute. Cerci short and stout. The penis valves and volsellae have not been dissected from the specimen.

Forewing venation (Fig. 5) of the *Solenopsis* type, as in *Orectognathus*, the apical elements (Rsf 5, Mf 4 and Cu-A) feebly developed, and the radial cell open. Hindwing narrow, with a broad posterior fringe of microtrichiae, and four well developed subapical hamuli; venation as in *Orectognathus*.

Head and most of alitrunk coarsely and closely punctate. Punctures of the pronotal dorsum and prescutellar area similar to the foveae of the workers, but almost contiguous. Sides of alitrunk with quite extensive shining areas, especially on the

median parts of the larger sclerites. Petiole and postpetiole with coarse punctures, those on the latter shallow and irregular. First gastric tergite semi-opaque, with very irregular and shallow large, flat, piligerous punctures.

Color blackish-brown; antennae, mandibles, under-mouthparts, and legs yellowish-brown. Wings clear, their veins pale yellow.

Described from a unique specimen collected with the holotype and its associated paranidotype worker series.

Material examined. Northeastern New South Wales: 2 miles east of Berry (type locality) December 28, 1959, holotype and 32 paratype workers, allotype male (B. B. Lowery). Burns Bay, Sydney, February 2, 1959, ex leaf litter, a single alate queen (paratype) (B. B. Lowery). Riverview College, Burns Bay, Sydney, April 19, 1959, eleven paratype workers (B. B. Lowery). Pymble, Sydney, March 18, 1956, a single dealate queen (paratype) (C. Mercovich). Barrington Tops, ex leaf mould (Berlese funnel sample), a single paratype worker (T. E. Woodward).

The holotype, with paratypes, has been returned to Father Lowery for eventual deposition in the Commonwealth Scientific and Industrial Research Organization collection at Canberra; the allotype, with paratypes, is in the Museum of Comparative Zoology, Harvard University; the remaining paratypes are in the Queensland Museum.

Biology. The following information regarding the biology and ecology of *M. browni* has been provided by Father Lowery.

The type locality is about two miles inland from Seven Mile Beach, in low hill country behind scrubby alluvial coastal flats. The collection was made in a grassed clearing in a heavily timbered area, with *Eucalyptus* and turpentine growing in black non-sandy soil.

The Riverview College locality overlooks Burns Bay, Lance River Cove, Sydney. The colony taken there was found nesting in damp yellow sand beneath a cover of moss and a little grass. The site was in a clearing in low scrub about 15 to 20 feet high, with *Eucalyptus corymbosa*, *Grevillea*, *Lantana* and *Leptospermum*. The soil near the nest contained a few small termite galleries and a large nest of the locally dominant ant *Acropyga australis*. The alate paratype queen was collected nearer the Burns Bay foreshore, wandering on leaf litter in warm sunshine, during the late afternoon.

Father Lowery has collected three further colonies of *M. browni* within 200 meters of the type nest site. One of these

colonies was nesting about four inches below the surface of coarse black sandy soil, under a small rock, but probably not in direct contact with it. A maze of termite galleries was located immediately beneath the rock, and permeated the surrounding soil.

The new species is dedicated to Dr. W. L. Brown, Jr. of Cornell University, a leading authority in ant taxonomy who has worked particularly with the Dacetini and has devoted much study to the Australian ants in general.

The addition of *M. browni* to *Mesostruma* requires no change in the basic concept of the genus, as formulated by Brown (1952). Indeed *Mesostruma* retains its appearance as a compact and distinctive genus, with its species abundantly distinct from each other.

Considering the characters of the worker and queen, *M. browni* seems to be most closely related to *M. turneri* Forel, which it resembles in the structure of the alitrunk, propodeal lamellae and petiole. It has a proportionately narrower head, however (see Brown and Wilson 1959, fig. 7), and lacks the longitudinal striation of the basal gastric segment seen in *turneri*. The absence of humeral denticles, and the general form of the alitrunk, propodeal lamellae and petiole distinguish *M. browni* from *M. laevigata* Brown. The new species differs from both the previously described species in its less dense sculpturing and overall glossiness, and its more extensive propodeal lamellae and more massive petiolar node. The three known species of *Mesostruma* may be separated by the following key (based on the workers).

1. Humeri rounded; dorsum of alitrunk strongly and evenly convex in profile; eyes protruding and very convex 2
   Humeri acutely subdentate; dorsum of alitrunk not so markedly convex in profile; eyes less convex and protruding only slightly. (Victorian mallee) ..... *M. laevigata* Brown
2. Head broad, CI 98-100; head capsule opaque, the foveae almost contiguous; gaster finely longitudinally striate over basal half or more of segment I (vicinity of Cairns, Queensland) ..... *M. turneri* Forel
   Head narrower, CI 88-96; head capsule strongly shining, the foveae separated by smooth areas at least as wide as their maximum diameter; basal segment of gaster smooth and strongly shining (northern New South Wales) ..... *M. browni* n. sp.

In the discussion above I have not considered the enigmatic species *?Mesostruma monstrosa* (Viehmeyer), 1925 (Brown, 1948). The unfortunate circumstances surrounding the original

selection of this species, which was based on an apparently abnormal specimen, have been discussed by Brown (1952). Dr. Brown now believes (personal communication) that Viehmeyer's species was most likely based on a defective *Epopostruma* specimen. In any case *monstrosa* seems best ignored, pending the location and competent re-examination of the type.

Codiomyrmex flagellatus new species

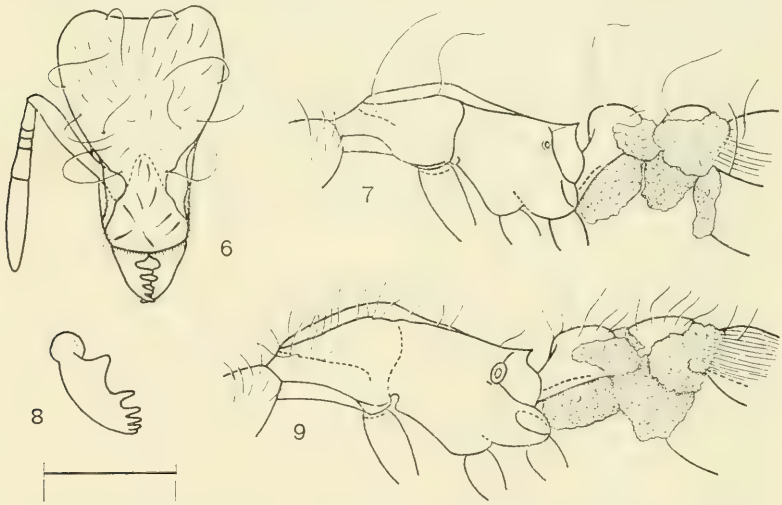
(Figs. 6-9)

Holotype worker. TL 1.9; HL 0.48; HW 0.32; scape length (SL) 0.23; ML 0.08; WL 0.47; CI 68; MI 19. General form much as in *C. semicomptus* Brown (1959) (Fig. 9), but smaller and more lightly constructed. Shape of head as in Figure 6. Dorsal surface of cranium convex, sloping towards occiput and clypeus as in *C. semicomptus,* the convexity less pronounced, however, and the occipital lobes more broadly rounded when viewed from the side (*cf.* Figs. 7, 9). Mandibles strongly convex, rising above the anterior clypeal border; with five strong, acute, conical teeth, each slightly smaller than the one posterior to it. Basal lamella normally hidden at full mandibular closure, set at a slightly lower level than the teeth and oblique to them; its shape as in Figure 8 — roughly right-triangular, the posterior edge almost perpendicular to the mandibular axis, and the anterior edge diagonal, forming the hypotenuse. The anterior lamellar edge rises almost immediately from the base of the proximal mandibular tooth so that the diastema is very brief. Clypeus almost perfectly plane.

Body profile somewhat as in *C. semicomptus,* with which it is compared in Figures 7 and 9. Alitrunk narrow, its maximum width 0.59 x the HW; its dorsum almost perfectly plane, without sutures or a median longitudinal carinula. Alitrunkal dorsum in side view evenly arched between the pronotum and the propodeal teeth. In dorsal view the sides of the pronotal disc are evenly rounded and those of the remaining alitrunkal dorsum almost parallel, with the distance between them, at the base of the propodeal teeth, slightly more than half the pronotal width. Dorsum of alitrunk margined with a fine carina, less distinct than in *C. semicomptus,* enclosing the pronotal disc anteriorly, and continuous with the upper edges of the propodeal spines posteriorly. The latter with their infradental lamellae similar to those of *semicomptus.* Propodeal spiracle minute, circular, its margin not appreciably expanded; it contrasts with that of *C.*

semicomptus, which is larger and has a wide and very conspicuous rim-like margin (Fig. 9). Profile of petiolar node as in Figure 7, shorter than that of *semicomptus*, only about as long as high in side view; seen from above the node is slightly longer than broad with rounded sides and a truncate anterior border. A full complement of areolate spongiform appendages is developed, distributed normally as in Figure 7. Gaster depressed; basigastric costulae reduced to about five feeble lines on either side of segment one, the two groups of costulae separated by a wide median shining area; the costulae extend back about $\frac{1}{10}$ the length of the segment.

Mandibles shining, with a few scattered punctures. Head capsule with a close cover of large, flat, irregular, shallow punctures, which are almost effaced in a small region in the center of the frons. Antennae very finely punctate, their scrobes punctate-granulose. Alitrunk, both nodes, gaster, legs and anterior parts of frons and clypeus smooth and strongly shining. Petiolar peduncle coarsely granulate.



Codiomyrmex flagellatus new species, Figs. 6-8, holotype worker. Fig. 6. Full-face view of head. Fig. 7. Alitrunk nodes and base of gaster in side view. Fig. 8. Mandible. *Codiomyrmex semicomptus* Brown, paratype worker. Fig. 9. Alitrunk, nodes and base of gaster in side view. Scale line: 0.16 mm., for Fig. 8; 0.25 mm., for Figs. 6, 7 and 9.

Occiput with a number of very fine long (0.05-0.08 mm.) hairs with clavate tips, somewhat finer than in *C. semicomptus*. Hairs of clypeus shorter and more distinctly clavate. A very few similar hairs are present on the anterior part of the pronotal disc and the dorsal surfaces of both nodes. The pilosity otherwise consists of exceedingly long (0.13-0.36 mm.), fine, tapering hairs, which are distributed symmetrically. On the head, five pairs in the following positions (see Fig. 6): on the occipital border, about halfway between its midpoint and its lateral extremity on either side; on either side and a little anterior to the median part of the frons; at the edge of the cephalic dorsum just anterior to its widest point; at the edge of the cephalic dorsum at about mid head length; on either side of the posterior extension of the clypeus, above the antennal insertions. On the body, six pairs: two pronotal; one on each node; two at the base of the gaster — distributed as shown in Figure 7. On the forelegs: a single flagellum on the outer side of the tibia, near its apex. On the middle and hind legs: single hairs on the outer sides of the limbs near the bases of the tibiae and basitarsi. These long flagella curve upward and inward on the head capsule; those of the body are erect with their apices turned posteriorly; the anterior pronotal and postpetiolar pairs are more tangential, and inclined laterally.

Type locality. Clump Point (near Mourilyan) Queensland, June 3, 1953 (T. E. Woodward), collected from a Berlese funnel sample of leaf mould.

Worker paratype variation. Seventeen worker paratypes, collected with the holotype, show no significant variation in size or structure. The specimens have at some time been subjected to drying and fungal attack while in alcohol storage, with the result that some are fragmentary. A few fungal hyphae are still attached to several of the specimens, and a number have had the pubescence, particularly the elongate flagella, damaged during the consequent cleaning.

Among the known *Codiomyrmex*, *C. flagellatus* is most closely related to *C. semicomptus* Brown, the only other known Australian species. The general resemblances between these forms are indicated in the accompanying figures. The two species may be readily separated by the characters discussed in the above comparative dsecription; the differences in size, pilosity, and propodeal spiracular structure are especially characteristic.

The adaptive significane of the peculiarly sparse and elongate body pilosity of *C. flagellatus* is not understood, and deserves examination should live material become available for future study.

The holotype, with paratypes, has been placed in the collection of the Queensland Museum. Paratypes are deposited in the Museum of Comparative Zoology, Harvard University, and the Commonwealth Scientific and Industrial Research Organization Collection, Canberra.

I wish to acknowledge the generous assistance of Father B. B. Lowery of Sydney, and Dr. T. E. Woodward, of the University of Queensland, who collected the bulk of the material cited above and made it available to me for study. I wish also to thank Dr. E. O. Wilson, of Harvard University, for his assistance and advice during the preparation of this paper.

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BREVIORA

Museum of Comparative Zoology

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ANOLIS SCRIPTUS GARMAN 1887, AN EARLIER NAME FOR *ANOLIS LEUCOPHAEUS* GARMAN 1888

By A. STANLEY RAND

Garman in 1887 described *Anolis scriptus* on the basis of five specimens in the Museum of Comparative Zoology, giving the type locality as "Silver and Lena Keys, Fla." Barbour in 1914 re-examined Garman's type series and decided that they were identical with *Anolis cristatellus* from Puerto Rico and the Virgin Islands and therefore placed *A. scriptus* in the synonymy of *A. cristatellus*. In the course of an examination of the Museum of Comparative Zoology anoles referred to *A. cristatellus* I had occasion to study the type series of *A. scriptus*. I find that the series is mixed and none is *cristatellus*. One, a juvenile, is *A. homolechis quadrocclifer* of Cuba; the other four are conspecific with the form from the southeastern Bahamas described by Garman (1888) as *Anolis leucophaeus*, and apparently subspecifically identical with the form from the Turks and Caicos Islands now called *albipalpebralis* Barbour 1916.

Clearly the name *scriptus* can no longer be kept as a synonym of *Anolis cristatellus*, but correction of its status raises certain problems. Since the series is mixed a lectotype must be selected to fix the name.

The type series, three adult males and two juveniles, are all somewhat faded from their long period of preservation. One of the juveniles possesses the scale characters of *Anolis homolechis* and the color pattern, dark spots over the shoulders, is still sufficiently evident to identify it as *Anolis homolechis quadrocclifer*. This is the specimen labeled as coming from Lena Key, which thus would appear to be Cayos de la Lena, near Cabo San Antonio, Cuba.[1] I have arbitrarily excluded this juvenile from the

1 For further information on this form see Ruibal and Williams (1961).

concept of *A. scriptus* and it therefore needs no further discussion.

The remaining four specimens seem to belong to a single species and I herewith designate M.C.Z. No. 65950 as the lectotype of *Anolis scriptus* Garman.

The labels accompanying these specimens say "Silver Key Florida." I, like Barbour, have been unable to locate a Silver Key anywhere in the West Indies. There is a Silver Bank near the islands from which the types must have come in the southeastern Bahamas but it is completely submerged.

These specimens are very like *cristatellus* as both Garman and Barbour agreed. Garman distinguished them from *cristatellus* on the basis of the greater size of the two paravertebral scale rows. Barbour (1914, p. 274) said, "I can not see, however, that these are at all enlarged; and there is no other character in which they vary from true *A. cristatellus*." An examination of the type series helps to explain this contradiction. Two of the males have the two paravertebral scale rows enlarged more than is usual in *cristatellus*, but the third male has the paravertebral scale rows scarcely enlarged at all and it is undoubtedly this specimen that Barbour examined.

However, a close comparison shows certain other and more constant differences between the type series of *scriptus* and the many specimens of *cristatellus* examined. In *scriptus* the dorsal scales *lateral to the paravertebral rows* are larger than they are in specimens of *cristatellus* of similar size. In *cristatellus* also, the frontal ridges are higher and sharper and the frontal depression correspondingly deeper than in the type series of *scriptus*. Finally, in *cristatellus*, there are only 1-3 scales behind the interparietal and these are abruptly larger than the very small dorsal scales. In *scriptus* there are many more rows of enlarged scales in this position and they grade more gradually into the dorsal scales.

In all of these characters the type series of *scriptus* differ from *cristatellus* and agree with specimens of the species now called *leucophaeus*. So far as I can find, the types of *scriptus* do not show any scale differences from *leucophaeus*, nor does *leucophaeus* show any additional differences from *cristatellus*.

From this it appears that *scriptus* and *leucophaeus* are synonymous and *scriptus* as the older name must be substituted for *leucophaeus*.

The species "*leucophaeus*" is quite widely distributed in the southeastern Bahamas and has been divided into four subspecies. These races have been described primarily on the basis of color pattern, and they are all very similar in scalation. They are diagnosed in Table I.

The types of *scriptus* lack the many dark spots characteristic of *leucophaeus* and the lectotype has a well-developed tail crest which is lacking in *sularum*. Thus the name *scriptus* definitely does not apply to the populations called *leucophaeus* and *sularum*.

Distinguishing between *albipalpebralis* and *mariguanae* is more difficult. The diagnostic difference between them is the presence of a broad dark lateral band in *mariguanae*. This is absent in the type series of *scriptus* but it is also absent in many of the adult males of *mariguanae* and best developed only in the juveniles and females. Even the small "type" of *scriptus* lacks this band but this specimen is so faded that one cannot be positive that the band was never present. Many of the females of *albipalpebralis* have dark middorsal blotches which are lacking in the small "type" of *scriptus* but, since they are absent in many *albipalpebralis*, this is not conclusive. The male *scriptus* have a complex mottling along the sides in addition to a light narrow lateral line. The light lateral line is found in both *albipalpebralis* and *mariguanae* but the mottling in the types of *scriptus* is most like that found in *albipalpebralis*. Finally, the lectotype of *scriptus* has a dark line running posteriorly from the eye onto the neck. This marking is found in some of the males of *albipalpebralis* but in none of the *mariguanae* examined. So far as can be determined there are no useful scale differences between *mariguanae* and *albipalpebralis*. From this it appears that the "type" series of *scriptus*, while not indisputably assignable to either of these races, is most like *albipalpebralis* and the lectotype most clearly so. For this reason it seems necessary to replace the name *albipalpebralis* by the name *scriptus*. In accordance with this change the type locality of *scriptus* is restricted from "Silver and Lena Keys" to "Silver Key," Turks and Caicos Islands. Further restriction seems pointless at this time. The correct names for the races of this species now stand as follows:

Anolis scriptus scriptus Garman 1887 = *Anolis albipalpebralis* Barbour 1916

Anolis scriptus leucophaeus Garman 1888

Anolis scriptus mariguanae Cochran 1931

Anolis scriptus sularum Barbour and Shreve 1935

Table I. The subspecies of *Anolis scriptus*

	leucophaeus	scriptus = albipalpebralis	mariguanae	sularum
Range	Great and Little Inagua	Turks and Caicos Islands	Mayaguana	Atwoods Cay and West Plana Cay
Dorsal pattern	many small dark spots	narrow light lateral line; mottling	narrow light lateral line frequently bordered above by broad dark band	dark with salt and pepper pattern
Male tail crest	present	present	present	absent

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NOTES ON HISPANIOLAN HERPETOLOGY 5. THE NATURAL HISTORY OF THREE SYMPATRIC SPECIES OF *ANOLIS*

By A. S. RAND

The lizard genus *Anolis* is abundant in species and individuals in the Greater Antilles. Quite a number of the common species occur together over wide areas. There is thus a special opportunity to study the ecological relations of sympatric species of a single genus under conditions genuinely favorable for field observation.

Several papers have now been published which have begun to exploit this fortunate opportunity: Ruibal (1961) and Collette (1961) working on the anoles of Cuba; Oliver (1948) on those of Bimini in the Bahamas; Williams and Rand (1961) on the *semilineatus* group in Hispaniola. These and earlier workers — Grant (1940) for Jamaica; Stejneger (1904) and Schmidt (1928) for Puerto Rico and especially Mertens (1939) for Hispaniola — have established that in each well studied case there are small but definite differences in microhabitat among the sympatric *Anolis*.

In this paper I document the same point for the three commonest species of *Anolis* in Hispaniola. I describe also a number of behavioral differences which seem to be associated with the ecological differences and attempt to assess the adaptive significance of these behavior patterns. This study was made during a two-month field trip to the Dominican Republic and supplemented with observations on captive lizards kept in the laboratory in Cambridge.

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with transportation and other assistance in that country; Dr. Eugenio de Jesus Marcano who helped us in the field and who sent me live specimens on our return. I wish also to thank Mr. Clayton Ray for inviting me to accompany him on this trip, and for his assistance in the field; Dr. E. E. Williams for helping to arrange the trip and for his advice and assistance throughout, and Dr. A. L. Rand for critically reading the manuscript. Also I wish to thank Sigma Xi for providing some of the funds that made this trip possible.

MATERIAL AND METHODS

The field observations during the summer of 1958 were made incidentally to the main project, a survey of Dominican caves for vertebrate fossils. Consequently, they include no lengthy observations in any one locality but are a synthesis of data collected from widely separated places. Though I noticed no geographical variation in behavior, obviously this is a possible source of error that runs throughout the present study. This is particularly true as observations are lumped for different subspecies in two cases: *Anolis chlorocyanus chlorocyanus* and *A. chlorocyanus cyanostictus;* and *Anolis distichus ignigularis* and *A. distichus dominicensis.*

The main areas, where observations were made, were: Santo Domingo and vicinity, Santiago and the nearby Sierra Septentrional, Padre Las Casas, Sabana de la Mar and the mountains south of there, and the Sierra de Neiba. These field observations are least complete on *A. chlorocyanus* and uneven on the other two species. For example, I found eggs only of *cybotes,* while I observed copulation only in *distichus.*

The laboratory observations made at the Harvard Biological Laboratories involved only two species, *A. cybotes* and *A. chlorocyanus chlorocyanus.* These animals, ten of each species, all adults and about half of them males, were sent to me by Professor Eugenio de Jesus Marcano. The lizards were released in a room 12 x 20 ft. and 9 ft. high. The room was a constant 80° F. and lighted by a south window. Eight small tree trunks 7 feet tall, mounted on bases so that they stood upright, an 8 foot rubber tree, a potted pine bush, and some other potted plants were arranged around the room.

The lizards were fed meal worms on the floor and in dishes taped at various heights above the floor, on the tree trunks. Fruit flies were also released in the room. The whole room was watered daily.

For a period of about three weeks, daily observations of varying lengths were made. The lizards quickly came to ignore me as I sat quietly in one corner of the room and watched them with low power binoculars.

This was obviously not a natural situation but the observations that could be checked against the field notes show a gratifyingly close agreement. This method seems to be a useful adjunct to field observations though obviously no substitute for it.

All three of these species are small to medium sized lizards possessing the characteristic specializations of the genus: enlarged subdigital lamellae and a throat fan or dewlap that is best developed in the male. In each species the males grow to a larger size than do the females.

Anolis distichus varies in dorsal coloration from green to gray to brown, frequently with mottling on the back. The dewlap is yellow in *A. d. dominicensis*, and red with a yellow border in *A. d. ignigularis*. The males measure 51 mm in snout-vent length (Cochran 1941).

Anolis cybotes is dorsally gray or brown, sometimes reddish, frequently with two indistinct greenish lateral stripes. The dewlap is whitish or yellowish in color. The males measure 67 mm in snout-vent length (Cochran 1941).

Anolis chlorocyanus is usually bright green with the ability to change to brown. *A. c. cyanostictus* also has a rust-red spot in front of the shoulder and one on the head. *A. c. chlorocyanus* has a dewlap that is light blue anteriorly and dark, almost black posteriorly. *A. c. cyanostictus* has the dewlap proximally cadmium yellow, distally sky-blue. The males measure 71 mm. in snout-vent length (Cochran 1941).

OBSERVATIONS

The observations from both field and laboratory have been combined and arranged according to topics. Under each topic heading all three species are compared.

Geographical Distribution. All three species are widespread in the Dominican Republic. Apparently they avoid only the high, wet pine forests of the Cordillera Central and are less common in the dry regions on the south coast near Asua and in the northwest near Puerto Plata. However, *A. chlorocyanus* is replaced by *A. coelestinus* in the Barahona Peninsula. Geographical variation in each of these species has been described by Mertens (1939).

Habitat. I found these three species at almost every locality I visited in the Dominican Republic. Mertens called *distichus* and *cybotes* eurytopic forms and *chlorocyanus* only slightly less so. He records both *distichus* and *cybotes* from the mangrove areas along the coast to the lower pine forests around Constanza at some 1200 meters altitude.

The most significant environmental factor for all three species seems to be some sort of vertical perch, a tree trunk, fence post or cliff face, but *A. chlorocyanus* seems to avoid the most open areas.

Anolis distichus lives primarily on isolated trees and fence posts and along the edges of woods and trails and in open woods. *A. cybotes* lives in these situations but also occurs in the deeply shaded interiors of densely wooded areas that *distichus* avoids. *A. chlorocyanus* certainly occurs in the edge situations that *distichus* prefers and probably in the heavier woods as well.

Though there are differences such as these in the extremes tolerated, these animals live in the same habitats over most of the Dominican Republic and part, at least, of Haiti. Mertens notes that in separated localities he observed individuals of all three species living in the same tree. My observations agree with this.

Microhabitat. These three species, though living in the same habitat, have differences in their microhabitat preferences.

A. distichus lives almost exclusively on exposed (i.e. not closely surrounded by vegetation) tree trunks, fence posts and similar structures, within 10 to 15 feet of the ground. It is seldom seen on the ground or in the smaller branches of bushes or trees. Though it must descend to the ground to reach isolated trees, it does not spend much time on the ground. *A. distichus* is often very common on the palisade fences in small villages.

A. cybotes is also primarily an animal of exposed tree trunks and fence posts within 10 feet of the ground. However, it also frequents rocks and fallen logs and smaller individuals are frequently seen on the ground. It also avoids, during the day at least (see *Sleeping*), small twigs and foliage. These field observations are confirmed by the laboratory data which show *cybotes* spending most of its waking time on perches less than five feet from the floor.

A. chlorocyanus lives also on tree trunks and fences but unlike the other two, frequently ranges high in the trees and out among the smaller branches. I saw a female fall from the crown of a 30 foot palm tree. I suspect that this species is one that lives primarily up among the branches and ranges down the trunk

rather than the reverse. However, individuals were seen also on fences and once I saw a dozen individuals on a pole framework nine feet high that with a few bits of palm thatch was all that was left of a shed in the middle of a treeless pasture. Like *distichus, chlorocyanus* must occasionally descend to the ground to reach isolated trees.

In the laboratory, *chlorocyanus* spent most of its time high on the perches and ventured out among the leaves of the rubber plant much more than did the *cybotes.*

Territoriality. As Mertens noted, all three species appear to be territorial. He says that for *A. cybotes* and *chlorocyanus* he found only a single adult male and one or more females of each species on any one tree. When he placed an additional male on one of the occupied trees it was immediately attacked. *A. distichus,* he says, defends a smaller territory and the large trees may have several males, each with its own territory, as well as a number of females.

These observations agree with mine, although it was only in areas where *distichus* were extremely common that I found more than one adult male *distichus* on the same tree, and then only on large trees.

Certainly in the laboratory no male of either *cybotes* or *chlorocyanus* would tolerate another male of the same species in his immediate vicinity for long, and even females were chased away if they approached too closely. Occasionally a male of one species would display to an individual of the other species.

In addition to this horizontal effect a vertical stratification on individual trees or posts is evident in at least two of the species, *distichus* and *cybotes.*

On the smaller trees that were occupied by two individuals of *distichus,* the lizards were usually of opposite sex and the male was usually closer to the ground than was the female. On one tree there were four lizards of this species: a large male near the base, a female above him, a slightly smaller female above her and, highest of all, a juvenile who was about 7 feet above the ground. During the hour that I watched this tree all of the lizards moved a number of times but this stratification remained the same for it was actively enforced. When one of the higher individuals moved in sight of and within 2 or 3 feet of a lower one, the lower animal immediately reacted to it. The male did this by bobbing his head and pumping his dewlap, the female by a short charge in the direction of the intruder. In every case the intruder retreated immediately, around the tree and up.

In *cybotes* almost all of the individuals on the trees were large and most of them were males. The individuals that were seen on the ground were almost always juveniles or females; the females are much smaller than the males in this species. This spatial distribution seems to be a real phenomenon but I have no field evidence to support the hypothesis that it is the result of territorial defense. However, there are certain laboratory observations that support this contention. In the laboratory I saw no vertical stratification but I also saw no evidence that the females tended to spend more time on the ground than did the males. This may be because the perches were small and numerous enough so that each lizard could occupy its own, as they usually did. However, there was a definite stratification horizontally with the large males on the perches near the window and the smaller males and females on those farther away. When a smaller individual invaded a perch near the window, and this happened quite frequently, the resident male would display to it and the intruder would retreat. Thus, though there is no direct evidence that the distribution seen in the field is due to territorial defense, there is evidence that defense could be at least a contributing factor: the males taking the most desirable positions, the elevated perches, and chasing away any smaller individual that attempted to move in, with the result that the juveniles and females would spend most of their time on the ground.

It is of interest to note that this vertical stratification in *cybotes* and *distichus* results in greater difference in size between the individuals that occur together. Adult *cybotes* are larger, and the adult males much larger, than adult *distichus*. This size difference could be reflected in the size of the prey items taken and so reduce the competition for food between the two species. The young of *cybotes* are of course no bigger than adult *distichus* but these are the individuals that live primarily on the ground and so do not occur on the tree trunks with the *distichus*. The importance of this in reducing competition for food, if it acts in this way at all, is of course unknown. It would be interesting to have an analysis of the stomach contents of various sized individuals of each species.

In *chlorocyanus*, I have no clear evidence for vertical stratification either in the field or in the laboratory. However, the fact that most of the individuals caught on fences and tree trunks were adult males suggests that the females and the juveniles may

stay higher in the trees. This phenomenon may also give maximal emphasis to the size difference between this species and the *distichus* with which it comes in contact for it is the large individuals of *chlorocyanus* that descend the tree trunks and they meet first and presumably would compete most for food with the smallest *distichus*.

Posture. Seen in silhouette these three species are usually immediately recognizable. This is partly because of their different proportions but even more because of their very different postures.

A. distichus rests facing either up or down or angling across the tree with its head and at least the anterior part of its body well off the substrate and with its neck bent so that its head is parallel to the substrate but further away from it than are its shoulders (Cf. figure 4, plate 2, Mertens).

A. cybotes typically rests facing down the tree with the fore part of the body off the substrate and the neck bent dorsally so that the head is nearly parallel to the ground. In one individual seen resting on the underside of a log which slanted at about 45°, the neck was bent back well over 90°. This posture is true in the laboratory as well as in the field. On the ground the posture is much like that of *distichus* with the neck bent so that the head is parallel to the ground and raised above it.

A. chlorocyanus usually rests with both its head and body quite close to the substrate and its neck bent only a little if at all, both in the field and in the laboratory.

While these postures are typical of the normal resting position, both *cybotes* and *distichus* when mildly alarmed flatten against the substrate, and *chlorocyanus*, when about to display, raises itself up on its legs.

I believe these differences in posture can be correlated with feeding behavior as discussed below.

Mertens says that most *Anolis* rest with their heads pointing toward the ground. I noticed this most commonly in *cybotes* and less so in the other species.

Activity. A. distichus appears to be a much more restless lizard than either of the other two species. Like them it spends most of its time resting quietly but an individual seldom remains in one place for more than a few minutes. It then moves quickly a few inches away on its tree trunk and rests quietly again for another few minutes.

A. cybotes, on the other hand, seems to spend much longer periods of time resting in one spot. Again, when a change is

made, it is made quickly. In the laboratory when a *cybotes* moved from one tree to another, the lizard frequently ran down to the base of the tree, stopped for a few moments, left the tree with a jump and ran part way across the floor, paused, ran the rest of the way and with a jump started up the new tree, usually pausing again before settling down.

A. chlorocyanus, though also spending periods of time immobile, moved quite frequently, going slowly and deliberately about in the trees, in the laboratory as well as in the field. In the laboratory, moving from one tree to another was a single process. The lizard moved slowly down to the base of the tree, jumped off, dashed across the floor and with a jump started up the new tree. As little time as possible was spent on the floor.

Climbing. I have no observations on the climbing ability of *distichus*.

In the laboratory *A. cybotes* did not appear to be as sure a climber as *A. chlorocyanus*. I saw several of the former fall to the ground from the smooth leaves of the rubber plant while I noted that only one of the latter did so even though *chlorocyanus* spent much more time on these leaves than did *cybotes*. While both these species started their climbs in the lab with a jump up on to the vertical surface, and I saw a large male *cybotes* make a 6 or 7 inch vertical jump to reach a hanging branch, *chlorocyanus* made a great many more horizontal jumps. Particularly common was one used to cross the 10 inches that separated the two closest perches.

A. cybotes is apparently a quickly moving lizard, quite at home on the ground but not so much so in the more treacherous footing of smooth green leaves and small twigs. *A. chlorocyanus*, on the other hand, is shy of the ground, moving across it only occasionally and then with as much speed as it can manage, while in the less secure footing of more arboreal situations, its deliberate movements help keep it from falling.

Feeding. On several occasions a *distichus* was seen to move from its resting position on a tree trunk or fence post and snap up something small from the bark. Twice I saw a male interrupt his displaying to do this. Once I saw a male move up to an ant about an inch away, follow it up the tree a couple of inches and then apparently lose interest and turn away. Thus there seems to be some selection of food and not everything small that moves within range is eaten.

A. cybotes was never seen to catch anything in the field, though on two occasions I saw an individual struggling with a large dragonfly; each time the lizard had the head and thorax in his mouth and the wings and abdomen still protruding. In the laboratory, *cybotes* came willingly to the floor to take meal worms. Sometimes a lizard would return to a tree to eat the meal worm but usually it remained for several additional minutes before returning either to its old tree or a new one. I never saw a *cybotes* moving around on the floor looking for food. On one occasion a male left his perch and ran about 10 feet across the floor to make an unsuccessful attempt to capture a 2-inch cockroach.

I have no data on *chlorocyanus* feeding in the field. In the laboratory several individuals were seen snapping at small objects on the leaves and twigs. This species only rarely came down to the floor to capture meal worms and each time that one did so it moved slowly to the base of the tree, then rushed out, seized the meal worm, ran back and climbed up the tree before stopping to eat its captured prey.

On the basis of this limited evidence, some tentative generalizations about the relations of feeding, posture and movement can be made.

A. distichus seems to feed primarily on smaller insects that it catches on the tree trunk. The posture with the head held high above the substrate would enable it to see more of the tree trunk than it could if the head was held low. The frequent movements are necessary if the lizard is to take advantage of the insects that happen to be on the opposite side of the tree trunk. The head is held parallel to the surface in which the lizard is most interested.

A. cybotes males get at least part of their food from the ground after sighting it from their elevated perch. The posture of this species keeps the head roughly parallel to the surface in which the lizard is most interested, in this case the ground. Since the lizard can see a large sector of the ground around him at all times, he need not change his position frequently to maintain a careful scrutiny of a considerable area.

A. chlorocyanus almost certainly gets most of its food from the trees in which it usually lives and its slow movements suggest that at least part of the time, unlike the other two species, it goes looking for it instead of lying in wait. The head is held parallel to the surface in which it is most interested.

We need more observations on all of these points and particularly on the feeding of *A. chlorocyanus*. But it is interesting that the two species, *distichus* and *cybotes*, that occur in the same microhabitat, on the tree trunks, seem to differ so markedly in feeding behavior.

Mertens remarks, in passing, that most *Anolis* get their food on the ground and among the roots of the trees and that their usual posture, as he records it, oriented toward the ground, may be related to this. I believe that this is true of *cybotes* but not of the other species.

Escape. Each of the arboreal species has a noticeably different method for evading herpetologists and presumably other predators.

A. distichus, when approached, quickly moves around to the other side of its tree trunk, usually moving up or down at the same time. If followed, the lizard may continue this maneuvering to keep the tree trunk between itself and the pursuer for some minutes. Soon, however, the lizard will either run up the tree out of reach or run down it to the base where it is concealed by the surrounding vegetation. Only when very hard pressed will one leave his tree or post and run out into the grass. Occasionally, and this was noted especially early in the morning, *distichus* would hide under a bit of bark or in a hole in the tree. Mertens says that *distichus*, when approached, runs around to the other side of its tree or post and then down to its base to hide. He does not mention any of the other behavior described here.

A. cybotes showed the same tactics in the field and in the laboratory. When approached, an individual would remain still until I came very close, then suddenly it would dart around to the other side of the tree; it might stop there but only until I moved into view again, then, instead of employing evasive action on the tree, it would usually run down and, unlike *distichus*, frequently leave the tree completely. In the laboratory the lizard usually ran a few feet away, where it might remain on the floor for some moments or might immediately climb a new tree. Mertens records these same flight reactions for this species. An *A. cybotes*, discovered on the ground or on a fallen log, frequently hid under whatever cover was available. Sometimes a large male, when first approached, would display his dewlap to me before fleeing. This was observed occasionally in the wild and became very common with one male in the laboratory after he became accustomed to me.

Usually in the field, *chlorocyanus,* when approached, immediately began to climb up the tree. This action was slower and more deliberate than that of the other two lizards but, since it was started sooner, the lizard was usually carried safely out of my reach. In the laboratory and in the field, when on a fence, where the lizard could not climb out of reach, it usually climbed as high as it could get and then dodged about there. Only very occasionally did one run down to the ground, though frequently one jumped to a nearby perch, if available, or ran out among the foliage and twigs at the ends of the branches. Mertens also notes that *chlorocyanus* usually climbs up its tree and conceals itself in the crown.

The escape behavior of the three species closely parallels the feeding behavior. *A. distichus* conducts its evasive behavior on the tree trunk. *A. cybotes* willingly leaves its perch to escape on the ground, and *A. chlorocyanus* retreats whenever possible up into the top of the tree.

Daily Activity. Since I did not spend long periods of time watching any one lizard or groups of lizards, I have no detailed information on the variations in activity during the day.

All three species seem to be strictly diurnal. They were seen sitting in the sun more frequently in the early morning than at other times of the day, presumably to raise the body temperature to the preferred level. *A. distichus,* at least, seems to feed more actively in the morning than at any other time. On several occasions I captured one with food in its mouth and three times I had one snap at the knot of the thread noose with which I was trying to snare it.

Sleeping. I do not know where *A. distichus* spends the night but, since individuals sometimes use holes in trees as hiding places in the early mornings, they may possibly use these during the night.

Two individuals of *A. cybotes* were found asleep at night, in the field. Both of them were males and were asleep on top of the foliage of the outermost twigs of small bushes. They were plainly visible from my vantage point, though perhaps not to a predator, such as a snake, climbing the bush. In the laboratory one evening during an examination of the room, I located seven *cybotes* asleep. Five of them were in the needles at the tips of the branches of the pine bush, one on a small vine where it stretched away from the tree trunk, and the last on top of the topmost leaf of a large-leaved potted plant. Shaking a branch on

which a *cybotes* was sleeping woke the lizard but it did not move until the branch was shaken vigorously or the lizard touched. Then it jumped immediately to the floor and remained there unmoving.

A. chlorocyanus was seen asleep only in the laboratory where during the period mentioned above I located six animals. Three of them were sleeping between large leaves of the rubber plant and the wall, one was between a board and the wall, one inside a cold radiator, and only one exposed, on top of its perch. When disturbed, the *chlorocyanus* immediately sought new hiding places.

As Mertens notes, *A. distichus* and *A. cybotes* sleep with their hind legs partly flexed, while *chlorocyanus* usually sleeps with them extended along the tail.

I do not know enough about the real and potential nocturnal predators of *Anolis* to speculate on the adaptive significance of these sleeping places. But it is striking that they are so different from the situations in which the animals spend the day. Male *cybotes*, which in the daytime live on substantial vertical surfaces, during the night sleep on the small flexible foliage and twigs of bushes and vines. *A. chlorocyanus* during the day is usually exposed to view and during the night sleeps under or behind some sort of cover.

Reproduction. Since copulation was observed only in *distichus* and eggs found only of *cybotes*, it is not possible to compare these species with respect to reproductive behavior. I am including these data in the hope that eventually comparative data will be available.

Three times pairs of *distichus* were seen in copulation in early to mid-afternoon on tree trunks from four to six feet above the ground. In no case was the preceding courtship observed. In one case the lizards were oriented diagonally up a large tree six feet from the ground. The larger male was on the higher side and on top of the smaller female. One of his front legs was across her shoulders and holding on to the tree in front of her front leg; one of his hind legs was across the base of her tail, the toes resting on her thigh and the trunk in front of it. His other legs were spread out holding the tree. His tail was bent under hers and his head was resting on but not biting her neck. Her position was that of any resting lizard except that her tail was strongly arched. The position observed in the other cases was virtually identical.

SUMMARY AND CONCLUSIONS

These observations on the behavior and ecology of these three species of lizards, *Anolis distichus*, *A. cybotes* and *A. chlorocyanus* in the Dominican Republic are obviously incomplete. However, certain tentative conclusions can be advanced.

These species are sympatric and occupy the same macrohabitats over much of their ranges. The species differ somewhat in their microhabitats but they are not clearly separated spatially in this way; members of each species occur on the same tree within feet and sometimes within inches of each other. They all have the same basic body form, though differing somewhat in size, in proportions and in morphological adaptations such as development of the enlarged subdigital pads. They are all insectivorous in diet. However, in the details of their behavior they are very different. These details can be fitted together to form a picture of three morphologically similar species of the same genus living together in the same habitat but living three very different lives.

Reviewing these very briefly, *Anolis distichus* is strictly an animal of the lower tree trunks. Its territorial pattern results in spacing out the individuals living on the same tree with the largest at the bottom and the smallest higher up. This species feeds on small insects on the trunk, utilizing a posture and pattern of activity that enables it to forage effectively in this sort of place. When frightened it takes evasive action on the tree trunk, and copulation takes place there.

A. cybotes, though partially an animal of the tree trunks, is also closely associated with the ground below. Its territorial behavior results in a spatial distribution with the large individuals on the trees and the smaller ones on the ground. Even for the individuals on the trees the perches there seem to be primarily lookouts from which to survey the ground. The postures and patterns of activity seem fitted best for this and much less so for watching the tree on which the lizards sit. Certainly they do go to the ground to capture food spotted from these perches. They run to the ground when frightened and they bury their eggs in the ground.

A. chlorocyanus in its behavior seems as closely related to the tree tops as *cybotes* is to the ground. It seems to be mainly the large males that descend the tree trunks. Some feeding undoubtedly occurs high in the trees even in these large males and

chlorocyanus retreats upwards when frightened. Its slow deliberate movements seem adapted to the more precarious arboreal footing among the leaves and twigs.

These are not just three similar animals doing the same things in the same way in slightly different places but three similar animals, each with a unique set of complex behavior patterns which interlock functionally so that each species has its own way of life within the same habitat.

This situation can be an example of the operation of the Gause-Volterra hypothesis that closely related species can live together only if they differ in ecology.

Since many of these differences can be correlated with feeding behavior they can be interpreted further as serving to reduce interspecific competition for food.

However, the demonstration that these conclusions are valid must await the collection of further data, particularly data on just what environmental factors act to limit the population densities of each species.

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NOTES ON HISPANIOLAN HERPETOLOGY
6. THE GIANT ANOLES

BY ERNEST E. WILLIAMS

INTRODUCTION

Mertens (1939) has called attention to the existence of geographic variation in the giant anoles of Hispaniola and has distinguished a typical western race, *Anolis ricordii ricordii* Duméril and Bibron, and an eastern race, *A. r. baleatus* Cope.

The distinction between these two forms is sharp and unequivocal; the situation is, however, more complicated than Mertens' limited sample (16 specimens) led him to believe. Study of the unreported series of Hispaniolan giant anoles in the American Museum of Natural History (AMNH) plus the specimens in the Museum of Comparative Zoology (MCZ) and the United States National Museum (USNM) (91 specimens in all) makes it clear that at least three vicariant forms are recognizable. The form occurring from Port-au-Prince *north* to Cap Haitien and Port-de-Paix is the one to which Mertens has shown that the name *ricordii* Dumeril and Bibron must be attached. Another, occurring in the north and east of the Dominican Republic, may be called, following Mertens, by Cope's name *baleatus* (*Eupristis baleatus* Cope 1864, Proc. Acad. Nat. Sci. Phila., p. 168, type locality "St. Domingo"). A third unnamed population occurs on the Barahona peninsula. A fourth population inhabiting the southwest peninsula of Haiti may be distinct. I list below the distinguishing characters of the three well-marked forms.

TABLE 1

ricordii	Barahona population	*baleatus* [1]
Very low nuchal and dorsal crests	Low nuchal and dorsal crests	A prominent nuchal crest, a variable but lower dorsal crest
Nuchal crest scales as long as or longer than high, and not or but little higher than the very low dorsal crest	Nuchal crest scales higher than long but *small*, not higher than the weakly developed dorsal crest	Nuchal crest scales much higher than long, always much higher than scales of dorsal crest
Head scales small, numerous (7-9 across snout at level of second canthal [2])	Head scales larger, fewer (4-6 across snout at level of second canthal)	Head scales large, few (2-5 across snout at level of second canthal)
In ♂ ♂ *deep black spots above shoulder*, sometimes also on occiput; no other evident pattern	Whole of body in both sexes with very *irregular small blotches and mottling*	Both sexes with no evident pattern or transverse *banding or reticulation*

CHARACTER ANALYSIS

The scales on the snout are swollen, bosslike in all Hispaniolan giant anoles. The differences are solely in the size of these bosslike scales. The contrast is extreme in this regard between the giant anoles of northern Haiti (*ricordii*) and those of the northern Dominican Republic (*baleatus*). The animals of the Barahona and southwestern peninsulas, however, are intermediate, overlapping in this regard the north Dominican (*baleatus*) and approaching the north Haitian populations. On this character alone it is not possible to separate every specimen of the north Dominican and the southern populations though there is a well-marked average difference.

Number of scales across the snout is a measure of a more general feature — general scale size — which is somewhat greater in *baleatus* than in *ricordii*. Mertens has cited a number of key regions, i.e. loreal region, base of the tail, etc., which show this.

1 A. Salle, who collected the type of *Eupristis baleatus* worked both in the northern Dominican Republic and at the base of the Barahona peninsula (map of travels compiled by W. J. Clench). It was therefore necessary to confirm the application of the name by checking the characters of the British Museum type. Miss A. G. C. Grandison has courteously confirmed that the nuchal crest scales of the type are indeed significantly higher than the dorsal crest scales.

2 I count the canthals forward from the anterior border of the orbit (see Fig. 1). The reverse count — from the anteriormost canthal back — is sometimes used, e.g. Oliver (1948). This, however, has the disadvantage that the scales here are small and variable and do not provide a stable starting point.

The snout, however, provides the clearest expression of this general feature and one which can be reduced to a simple count with an adequate numerical range (2-9). Mertens has used a similar transverse count but makes it directly in front of the eyes. I have chosen a transverse count somewhat further forward because this transverse line, anterior to the supraorbital semicircles seems to me more suitable as a place for a standard count utilizable for all species of *Anolis*.

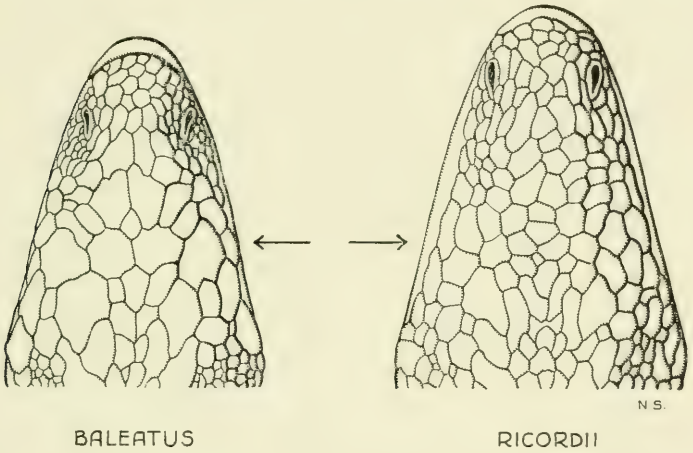

Fig. 1. The two extremes of anterior head squamation in *Anolis ricordii* subspecies. The arrows indicate the place at which the count across the snout is to be made.

The pattern of geographic variation of nuchal crest scales is not so simple. Again, the populations of Port-au-Prince and northern Haiti and northern Dominican Republic show the extremes, the crests of Port-au-Prince and of north Haiti populations very low with a long anteroposterior base, while those of north Dominican Republic populations are tapering, high, short based anteroposteriorly. The southern populations could again be described as intermediate but on careful examination this is not quite accurate. Both the north Haitian and southern populations have a reduced nuchal crest as compared with the north Dominican population but the nature of the reduction is different. The nuchal crest scales of north Haitian animals are long-based, low, rounded scales, not at all tapering; they are

sometimes shorter but usually slightly higher than the very low, long dorsal crest scales. In the giant anoles of the Barahona peninsula the nuchal scales are, in contrast, still short anteroposteriorly, relatively high, tapered, but *very small*, not appreciably higher than the tallest dorsal crest scales and notably smaller in area than the largest dorsal crest scales.

The few specimens from the southwestern peninsula do not permit adequate analysis of the populations of this important geographic area. The four adults examined all come from the vicinity of Fond des Negres halfway along the peninsula. In squamation, these are very like the animals of Port-au-Prince and north Haiti. The one remaining specimen is a juvenile (78 mm snout-vent length) from the foothills of the Massif de la Hotte. Although it is less than half-grown, its dorsal and nuchal scales are appreciably higher and less broad based than those of the adults from Fond des Negres and indeed are very comparable to those of the Barahona population; in addition, in this individual these scales are double and even triple even on the nape. It thus seems very possible that the populations of the middle of the southwest peninsula and those of its extreme end differ significantly. (See further discussion below.)

The nuchal crest scales seem in all populations to be somewhat variable. However, within each adequately-sampled population the range of variation is very characteristic and does not blur the distinctions tabulated above. Despite statements by Boulenger (1885) and by Mertens (1939), I do not find a clear correlation with sex; females, for example, of *baleatus* do not consistently have lower nuchal crest scales than male *baleatus* of the same size. There is, however, clear ontogenetic change; the smallest individual of *baleatus* at hand (AMNH 28651 from San Juan Bay, Samana, 41 mm snout-vent length) has the nuchal crest scales only incipiently enlarged and could not be recognized as a member of the *baleatus* population on that character. However, in *baleatus* the characteristic, tapering, spinelike nuchal scales develop very early and even specimens little more than half grown (e.g. MCZ 57719, Santiago, ♂, 83 mm snout-vent length; MCZ 5445, Samana Peninsula, ♂, 88 mm snout-vent length) are very readily recognizable.

Dorsal crest scales are more variable than nuchal crest scales, and variable in a peculiar fashion: there is sometimes a regular alternation of relatively high triangular single scales and pairs

of much lower, more quadrangular scales.[1] However, such a regular alternation occurs — if present at all — on only a portion of the back and there is present between nuchal crest and dorsal crest, on the one hand, and dorsal and tail crests, on the other, various irregular conditions with double and single crests erratically intermingled and scale types somewhat intermediate and rather irregularly so. In *ricordii* itself with a very low dorsal crest the double condition with all low scales is most frequent; in *baleatus* the situation is individually very variable; in the Barahona and the southwest peninsulas the double condition of the dorsal crest predominates.

The body color of live specimens and well-preserved alcoholics is probably useful. The usual specimen, however, requires much interpretation and its evidence must be received with some skepticism. In tabulating pattern, above, I have ignored all ill-defined discolorations and have tried to assess pattern on the basis of real aggregations of pigment rather than fortuitous darkening of random areas by formalin. Even with this qualification the problem is not simple: these are *Anolis* and have the power of color change; an adequate discussion of their pattern would be possible only if the whole repertoire of color changes were known. I record my information below by population.

Ricordii: Females from Port-au-Prince and north Haiti appear to be plain green above with no markings of any sort. Males from Port-au-Prince are also mainly green (as preserved they may show an obscure, very fine brown reticulation) but are distinguished by a large, very characteristic patch of black above the shoulder but of ill-defined shape and varying extent. There may also be irregular black patches extending onto the back of the head. There may also be a white patch at the corner of the mouth. A Cap Haitien male (Senckenberg 10445) is quite similar to Port-au-Prince specimens. Of three males newly received from Ti Guinin a little to the east of Cap Haitien (MCZ 66147-9) two have almost no black at the shoulder (only small and inconspicuous spots) and none at all on the head. The other male is as devoid of black spotting as any female. All show fine brown reticulation quite like that of similarly preserved Port-au-Prince males.

1 In the tabulation above I have compared the nuchal crest scales with the highest crest scales at midbody.

Baleatus: Schmidt (1921, p. 10) records specimens from Sanchez and Villa Rivas as "usually green with dark-edged transverse bands of light greenish yellow." Preserved specimens which have any definable pattern show this transverse banding which is present on dorsum, limbs and tail; it appears to be most persistent on the tail. It is very conspicuous in a specimen near hatchling size (AMNH 28651). There are frequently numbers of small spots on the sides of the belly and on the venter. The MCZ Santiago series, though preserved in a light phase, show very irregular light banding much invaded by dark reticulations, but the bands are very prominent on limbs and tail.

Barahona Population: I have unfortunately been unable to find any description of Barahona giant anoles in Hassler's notes. I must therefore rely entirely on the preserved specimens, which, however, are unusually consistent, though from several localities and with very different collection dates. Collected by Hassler, they differ strikingly from the *baleatus* specimens, most of which were also collected by Hassler. All Barahona specimens, and most clearly those from Valle de Polo, show irregular small blotches, very variable in tint and extent, scattered over the entire dorsum. The closest approach to this condition is seen in those *baleatus* which show reticulation. There are never in the Barahona specimens the large shoulder spots of *ricordii, sensu stricto.*

One specimen (AMNH 51241 from Enriquillo) does show transverse banding, but more obscurely than in *baleatus.* The small blotches are also very obscure in this specimen, which therefore could not in this phase be recognized as a member of the Barahona population on its color. The nuchal and dorsal crest scales are, however, typical *barahonae,* and the hypothesis which I have adopted is that the blotching so characteristic of most preserved specimens is characteristic only of one of the phases of the color repertoire possible to this population.

Population of the Southwest Peninsula of Haiti: Again the material is inadequate for proper analysis, the more evidently so since the few available specimens suggest that this is not a unit sample. The juvenile from the Massif de la Hotte is, as preserved, reddish or purplish brown with indistinct broken dark longitudinal lines on head and nape and more evident narrow brown transverse bands on the back, six between shoulder and groin, in pairs with very slightly lighter reddish-brown between each pair. The tail is obscurely annulate.

In contrast, the three adult females from the vicinity of Fond des Negres are essentially patternless (MCZ 66016 is dark and obscurely vermiculate, and USNM 72631, 72633 are plain light green except for a subocular half ring of scales that is conspicuously white). The single male is similarly nearly patternless but has also the subocular half ring of white and, in addition, a series of small black spots above the shoulder, very like a vestige of the large black shoulder spot of Port-au-Prince animals and very like those of the two Ti Guinin males.

TAXONOMIC EVALUATION

There appear to be at least three distinctive populations of giant anoles, all readily separable by nuchal crest development and body color, less sharply separable by the size of the scales on the snout. These populations are allopatric and thus may be species or subspecies.

The differences between typical *baleatus* and typical *ricordii* are such that they could well imply specific distinction. However, all the populations south of the Cul de Sac Plain, both the rather distinctive Barahona animals and the very poorly known populations of the southwest peninsula, are to some degree intermediate between the two northern extremes although presenting some features that are their own. In thus bridging the morphological gap between the extremes, they strongly suggest that the Hispaniolan giant anoles belong to a single species.

The giant anoles are scarce and local. It is not to be expected that intergradation between the several populations will be easy to demonstrate; specimens from many of the critical intermediate areas are conspicuously lacking.

The Fond des Negres and Ti Guinin specimens, on the other hand, may be intergrade populations. The vestigial shoulder spots present in the two Ti Guinin males and the single Fond des Negres male suggest this conclusion, as does, in the latter case, the combination of nuchal and dorsal squamation most like typical *ricordii* with somewhat lower scale counts across the snout. No giant anoles are at hand from the northwest Dominican Republic. This is the area in which intergradation between *ricordii* and *baleatus* is to be expected. It is thus not at all surprising to find the first suggestion of loss of characters of the typical race just to the east of Cap Haitien.

On the southwest peninsula, the Fond des Negres area is one in which such intermediate populations are to be expected, as recent collections from the area show. Thus, *Dromicus parvifrons parvifrons* and *D. parvifrons protenus* appear to meet in this area and several anole races (to be reported later in this series) show intergradation at just this point.

I thus interpret the Fond des Negres giant anoles as intergrades between typical *ricordii* and a population to the west occupying the tip of the southwest peninsula. This western population I infer to be represented at present by the single juvenile specimen collected by P. J. Darlington in the foothills of the Massif de la Hotte.

The wide-banded specimen from Enriquillo in Barahona is reminiscent of the banded color phase in typical *baleatus,* but in squamation it is not intermediate and it is geographically quite unsuitable as a member of an intergradient population. Nevertheless, the presence of this color phase hints at a closer relation with *baleatus* than otherwise could be inferred.

The absence of other evidence or hint of intergradation is easily accounted for by the gaps in the distributional record, and, granted the desirability of further evidence, recognition of subspecies status seems justified for typical *ricordii,* for *baleatus,* for the Barahona population and probably also for a population at the west end of the southwest peninsula of Haiti. The latter two populations are currently nameless. That from the southwest peninsula is at the moment very insufficiently known, and it would not now be appropriate to describe it. The Barahona population, on the other hand, is well recorded and may be formally named:

Anolis ricordii barahonae new subspecies

Type: MCZ 43819, Polo, Valle de Polo, Barahona, Dominican Republic, an adult female collected by W. G. Hassler, September 1932, J. C. Armstrong donor.

Paratypes: Valle de Polo, MCZ 56141, AMNH 51036, 51235-6; *Herman's Finca near Paradis,* AMNH 51231-3; Barahona, AMNH 50255-6, 50261; *Halfway between Trujin and Enriquillo,* AMNH 51230; *Enriquillo,* AMNH 51241.

Diagnosis: A subspecies of *ricordii* distinguished from the typical form and from *baleatus* Cope by the nature of the nuchal crest (formed by small but slender tapering scales not or very

little higher than the highest scales of the dorsal crest), by the size of the scales of the snout (4-6 across snout between second canthals), and by a characteristic phase of coloration in both sexes in which small blotches are present, irregular in shape and of varying intensity.

List of Specimens Examined: A. r. barahonae (17 specimens). DOMINICAN REPUBLIC. *Polo, Valle de Polo:* MCZ 43819; *Valle de Polo:* AMNH 51036, 51235-7, MCZ 56141; *Barahona:* AMNH 50255-6, 50261; *Herman's Finca near Paradis:* AMNH 51231-3; *Halfway between Trujin and Enriquillo:* AMNH 51230; *Enriquillo:* AMNH 51241; locality uncertain: AMNH 51229, 51234, 51240.

A. r. ricordii (12 specimens). HAITI. *Port-au-Prince:* AMNH 49501; *Diquini:* MCZ 8619, USNM 118902, 123988; *Source Leclerc, Morne Decayette, near Port-au-Prince:* MCZ 65729-31; *Petionville:* MCZ 60013-4; *Marcaco:* USNM 69437; *Port-de-Paix:* MCZ 63338; *Ti Guinin near Cap Haitien:* MCZ 66147-9. [Records by Mertens: *Port-au-Prince,* 4 specimens; Cap Haitien, 1 specimen.]

A. r. baleatus (57 specimens). DOMINICAN REPUBLIC: *Peña, near Santiago:* MCZ 57713-9; *Santiago:* MCZ 7831; *Las Bracitas:* AMNH 41465-6; *El Rio:* AMNH 41294, USNM 62104-5; *Rio San Juan:* USNM 74940-1; *Samana Peninsula* (various localities): MCZ 5445, AMNH 28651, 39807-15, 39817-23, 39825-9, 39837, 40224-30, 40387-90, 42285, 42775, 44841-4; *La Romana:* MCZ 16321. [Records by Mertens: *Santiago,* 5 specimens; *Moca,* 4 specimens; *Finca Arbol Gordo near Villa Altogracia,* 1 specimen.]

A. r. subsp. nov. (1 specimen). HAITI: *Foothills, Massif de La Hotte:* MCZ 38277.

A. r. subsp. nov. x *r. ricordii. Pemel near Fond des Negres:* MCZ 66015-6; *Fond des Negres:* USNM 72631, 72633; also 72632, skeletonized.

BEHAVIOR

The giant *Anolis* of Hispaniola is infrequently seen by collectors and consequently our information on its ecology and habits is limited. Such information as is available is summarized below by A. S. Rand. Quotation marks refer to Rand's personal observations.

A. ricordii ricordii, Morne de Cayette, near Port-au-Prince, Haiti (A. S. Rand and J. Lazell). "A large individual was seen about 15 feet up on a branch of a 30-foot high tree on the edge of a patch of brush on the hillside. It remained sitting quietly in sight for about half an hour until we climbed the tree to attempt to capture it. It then climbed out among the small branches where, despite an intensive search, we were unable to locate it again."

Port-de-Paix, Haiti (A. S. Rand and J. Lazell). "A female was seen sitting head down on the trunk of a large tree about 4 feet from the ground. The tree was one of a series forming a fence row. The lizard allowed us to approach and noose it."

A. ricordii baleatus, Pena near Santiago, Dominican Republic (C. E. Ray and A. S. Rand). "Local people who brought in a series at this locality reported that they lived among the upper branches of the larger shade trees in the coffee plantations."

Finca Arbol Gordo, Dominican Republic. Mertens reports that the single specimen collected by him jumped to the ground from the trunk of a palm tree. Mertens kept this animal in captivity for some time and wrote that it was active only in the late afternoon. When approached it squirreled around to the other side of its perch. It slept exposed on small branches with its hind legs flexed.

A. ricordii subsp., Camp Perrin, Haiti (A. S. Rand and J. Lazell). "A small boy guided Rand to a stand of coffee where a crowd of Haitians had treed a large individual. The lizard was about 20 feet up in a small tree. It was too high to noose and the tree too small to climb so we attempted to scare the lizard to a more favorable situation by poking it with a long pole. After considerable fuss the lizard ran out along a small branch to the next tree, down that to the ground, across the ground to hide among the roots of a large Cieba tree. After considerable prodding among the roots we dislodged the lizard which avoided the herd of assistants successfully and climbed the Cieba out of both sight and reach."

Above Maceline, near Camp Perrin (A. S. Rand and J. Lazell). "In a small stand of coffee we saw a single animal about 15 feet up in one of the large trees on a large branch. When Lazell climbed the tree it squirreled about the branch concealing all of itself except one eye. It then climbed up and out among the small branches and disappeared from view."

Mertens speculates that the giant anoles of Hispaniola were originally inhabitants of the lowland rain forest and have adapted to cultivated areas by living in the crown of the taller trees. The observations of Rand and Lazell tend to support this conclusion.

INTRAISLAND ZOOGEOGRAPHY

The portion of Hispaniola south of the Cul de Sac Plain, including the southwest and Barahona peninsulas and the La Selle and La Hotte ranges, has, as Mertens has emphasized, a number of endemic species and even genera. I have recently (Williams, 1961) stressed the importance of this area, which I have called the "southern island," in the initial differentiation of forms now widespread in the portion of the island north of the Cul de Sac Plain.

Barahonae as an isolate in "southern island" easily fits this pattern. *Balcatus* and typical *ricordii* do not.

This is merely the first of many examples to be discussed in this series which will show that not all the patterns of differentiation in Hispaniola can readily be explained by the simple hypothesis of "southern" and "main island" isolates. As in the present case so in a considerable number of others, there appear to be additional loci of differentiation, e.g. northern Haiti, which are not so evidently marked off by present or recently past barriers to distribution.

These cases of subsidiary loci of differentiation are not at present well analyzed. Hispaniola has not been really well collected, and it is now evident that the differentiation of local populations that occurs within it is finer grained than the sporadic collecting of the past could reveal. For many of the instances of minor loci of differentiation, data are just now being gathered.

RELATIONSHIPS OF *RICORDII* AND THE OTHER WEST INDIAN GIANT ANOLES

Anolis ricordii clearly belongs to the series of giant anoles that includes *equestris* of Cuba and *cuvieri* and *roosevelti* of the Puerto Rican-Virgin Island complex. *Anolis garmani* of Jamaica seems, even on externals, to show no features, except size, which specially link it to this group, and Richard Etheridge in an unpublished thesis (University of Michigan) has shown that osteologically it belongs to quite a different section of the genus.

No full study has ever been made of the Greater Antillean giant anoles as a group, though they clearly merit such a study.[1] I do not intend to attempt this here, but in order to place the races of *ricordii* within a frame of reference which might add to our understanding of them and of their origin I have compared all of the species for a number of mostly qualitative characters which were simple to determine and to evaluate. Table 2 presents the results of this comparison.

It is sufficiently clear even from the limited evidence presented by Table 2 that we are dealing with four good species. The Hispaniolan populations are a unit as compared with the forms of the neighboring islands and, as in the case of the other polytypic giant anole, *A. equestris*, the intraisland differentiation has involved primarily scale size and color pattern.

There is one unusual zoogeographical feature in the distribution of the giant anoles — the occurrence of *A. cuvieri* and *A. roosevelti* on the same island bank, *cuvieri* on the mainland of Puerto Rico, *roosevelti* on Culebra in the Virgin Islands. These two are very distinct species. Their differences are at another level than those between *ricordii* and *baleatus*, and their occurrence on what must at various times during the Pleistocene have been a single land mass provides a special problem in accounting for their origin and dispersal.

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1 For further information on the non-Hispaniolan species see Stejneger (1904), Grant (1931), Schwartz (1958).

TABLE 2

Character	*equestris*	*ricordii*	*curieri*	*roosevelti*
Head scales	Swollen, very rugose	Swollen, keeled or wrinkled	Relatively flat, keeled	Swollen, keeled
Scales across snout	2-5	2-9	6-8	6-8
Frontal depression	None	Shallow	Shallow	Deep, bounded by ridges
Interparietal from supraorbital semicircles	4-5 Scales swollen	4-6 Scales swollen	3-5 Scales with multiple tubercles	2 Scales smooth, flat
Sublabials	Sublabial row well differentiated, scales smooth	Sublabial row well differentiated, scales smooth	Sublabial row *not* differentiated, scales often multicarinate	Only anteriormost sublabial on each side differentiated, scales smooth
Postanals	Present in ♂	Present in ♂	Present in ♂	*Not* present in ♂
Scales under base of tail	Smooth	Smooth	Keeled	Smooth
Scales on side of base of tail	Small, quadrate arranged in regular vertical rows	Small, quadrate arranged in regular vertical rows	Rather large, irregular in shape and arrangement (Cf. figs. 87 and 88, Stejneger, 1904)	Small, quadrate arranged in regular vertical rows
Scales on limbs and digits	Smooth	Keeled	Keeled	Keeled
Lamellae under 4th toe (approximate)	45	31	33	33
Snout-vent length, adult ♂	157 mm	137 mm	135 mm	160 mm

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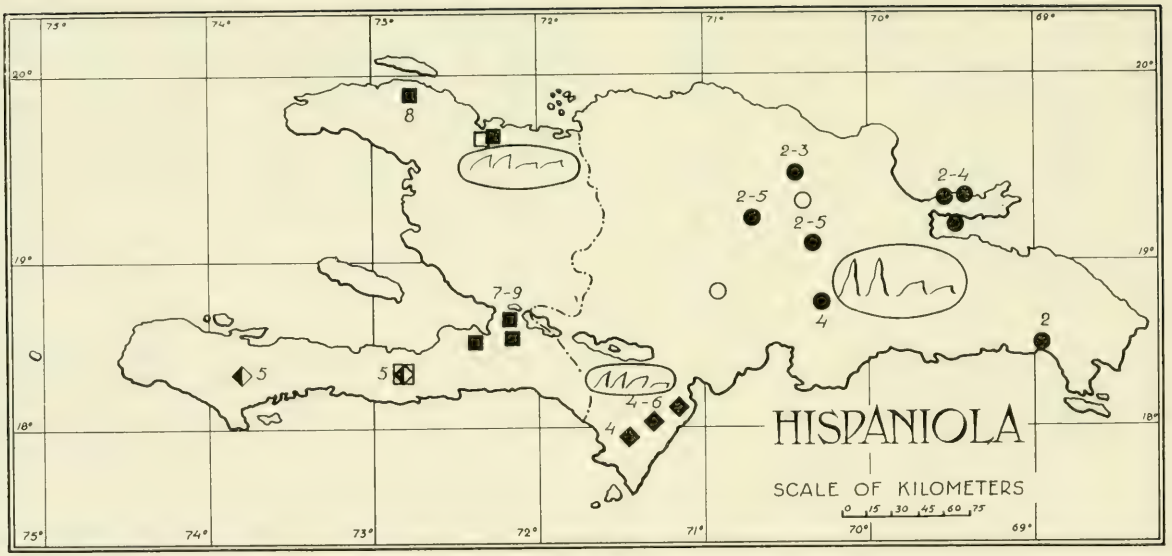

Distribution of *Anolis ricordii* subspecies. Hollow symbols for *ricordii* and *baleatus* are Mertens' records. In each oval is represented, left to right, the outline of two nuchal scales and two of the lower dorsal scales. Numbers are counts of scales across snout in populations indicated by adjacent symbols.

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THE FOSSILIFEROUS TRIASSIC DEPOSITS OF ISCHIGUALASTO, ARGENTINA, AND PRELIMINARY DESCRIPTION OF *ISCHIGUALASTIA*, A NEW GENUS OF DICYNODONT

BY ALFRED SHERWOOD ROMER and C. BARRY COX

THE FOSSILIFEROUS TRIASSIC DEPOSITS OF ISCHIGUALASTO, ARGENTINA

BY ALFRED SHERWOOD ROMER

Early in 1958, a joint expedition of the Muséo Argentino de Ciencias Naturales of Buenos Aires and the Museum of Comparative Zoology, Harvard University, was organized to explore continental deposits in the western Argentine in search of fossil vertebrates. The personnel included, for the Buenos Aires Museum, Dr. Guillermo del Corro, geologist, and Mr. Orlando Gutiérrez, assistant; from Harvard, Professor Bryan Patterson, preparators Arnold C. Lewis and James Jensen, Mrs. Romer and the writer. The earlier part of the trip was spent in the general region of Mendoza. In late April it was decided to move our base northward and explore the valley of Ischigualasto.

This region lies some 300 miles to the northeast of Mendoza, in eastern San Juan Province, close to the border of La Rioja, in the department of Valle Fertíl, at a latitude and longitude of approximately 68°W, 30°5'S. No adequate maps of this area exist; Ischigualasto is shown on the San Juan sheet (no. 37) of the 1/500,000 map of Argentina, but the details are highly inaccurate. Frenguelli (1948, fig. 1, pls. 1, 2) gives sketch maps showing the general topography of the valley and its relation to adjacent regions. The name derives from an Indian village once

present at the margin of the valley. This, however, disappeared long since and the valley is completely uninhabited. In 1874 Stelzner (1885, pp. xii, 74-75) rapidly traversed the valley on mule-back, presumably following a trail which runs from Jachal, in San Juan Province, through the valley and on eastward to Patquia in La Rioja. Bodenbender (1911, pp. 94-113) similarly crossed by this trail several decades later. A small coal seam had been discovered in the hills west of the valley at a locality named los Rastros because of dinosaur-like footprints discovered there; Huene (1931) was taken, in 1927, on a hasty trip to see these footprints; he traversed the valley but was unable to stop there. Until recent years nothing was known of the geology of the region except for such observations as Stelzner and Bodenbender could make as they crossed it, and nothing of fauna and flora except the footprints just mentioned and a few plants collected by Bodenbender.

The reason for this former paucity of knowledge is obvious. The valley is extremely arid, and in the days of mule travel, a stay there was impossible because of the almost complete lack of water and fodder.[1] With the coming of automobile transportation and, particularly, of vehicles with four-wheel drive, the situation has changed radically, and in 1948 Frenguelli was able to publish a rather comprehensive account of the stratigraphy of Ischigualasto as the result of exploration of the area in 1943, primarily in the interests of paleobotany.

During the course of his work there, three fragments of cynodont skulls and jaws were recovered, and were described by Cabrera (1943). These were of interest as indicating the presence in Argentina of Triassic beds similar in fauna and presumed age to those of southern Brasil. But since so little reptile material was collected during Frenguelli's survey of the region, it seemed unlikely that work there would be profitable for the vertebrate paleontologist.

My attention was first called to Ischigualasto by Professor Huene before the results of Frenguelli's work became known. As noted above, Huene had crossed the valley on mule-back during his inspection of the los Rastros footprint site and, although unable to stop and prospect, had been struck by the

[1] Bodenbender (1911, p. 96) breaks off in the middle of his description of the region to insert a paragraph of emphatic and italicized warning: *"NOTA — A los futuros exploradores hago presente que no se puede contar . . . con suficiente pasto para los animales,"* etc.

seemingly favorable nature of the beds for vertebrate exploration. Like our Argentinian colleagues, I had failed to be impressed as to prospects by the few materials obtained by Frenguelli. A different light, however, was shed upon the possibilities by a publication by Heim (1949). He had been commissioned in 1944 to report on the los Rastros coal mine, but in crossing the Ischigualasto valley had become so interested in the region that a considerable part of his report is devoted to the Ischigualasto beds and, incidentally, to the fossils found there. He photographed a cynodont skull *in situ* (pl. VIII, fig. 2) and says (p. 22): "El señor de la Vega me llamó la atención sobre los restos de vertebrados que se han hallado frecuentemente en el suelo de las arcillas, especialmente en la parte media de la formación. Se presentan como acumulaciones de fragmentos de huesos, de color pardo oscuro. A veces aún se distingue la forma del cráneo y de la dentadura con restos de dientes negros, pero sin que se pueda restaurar esqueletos."

This report indicated that investigation of the Ischigualasto region might prove profitable, and our expedition moved to that region. A road of passable quality runs to Valle Fertíl, a village south of the valley, which serves as departmental capital. Beyond this, settlement is sparse and presently ceases altogether, the roads deteriorate into a confusing series of trails, and it was necessary to hire a local guide to reach our destination.[2] At Cerro Morado, about 50 km. north of Valle Fertíl, there is reached the southern edge of the valley which extends some 20 km. to the north-northwest. At its southern end its width is about 7 km.; it narrows to 2½-3 km. at the north. Its western boundary is a range of rugged sandstone hills, the eastern boundary an unbroken cliff of red sandstone, "los Colorados," striking in appearance, with a height, for much of its length, of 150 to 200 meters. The valley itself, almost bare of vegetation except for scattered thorn bushes, exhibits an expanse of shales of varied pastel colors and occasional sandstones. It is drained by a series of broad sandy arroyos which converge at about the center of its western margin where, at Agua de la Peña, there is a small stream of water (non-potable, according to our guide). From this point the deep gorge of the Rio de la Peña runs westward through the hills to the Rio Bermejo. Northwestward from

2 Since our work there, a new highway has been constructed that links Patquia with Pagancilla and Chilecito. This passes a little to the northeast of the Ischigualasto basin, rendering it comparatively accessible.

the main valley extends the narrower valley of the Rio de la Chilca, which turns westward to join the Bermejo.

We made camp near Agua de la Peña, began exploration of the valley — and were immediately astounded by the abundance of vertebrate remains which it contained. Every vertebrate paleontologist dreams of finding, someday, a virgin territory strewn with fossil skulls and skeletons. Almost never does this dream come true. To our amazement and delight, it did come true for us at Ischigualasto. All about us, in the clays of the valley, were exposed specimen after specimen of fossil reptiles. In most instances the greater part of the time of a field party is taken up in prospecting for specimens. Here little of this sort of work needed to be done, and our energies could be devoted to excavating the better specimens chosen from the wealth of materials readily available. Approximately six weeks were spent here. Our work was hampered by the shortness of the daylight hours at this season of the year, and by the fact that a number of trips to Valle Fertil, each taking a full day, were necessary to carry out fossil blocks and obtain food supplies, gasoline and water. Nevertheless, well over 100 specimens, mainly plaster blocks containing skeletons, partial skeletons or skulls, were recovered.

The geology of the region has been described by Frenguelli and by Heim, and discussed by Groeber and Stipanicic (1952, pp. 87-99). Apart from faults of a minor nature, the geologic structure is simple, the sediments uniformly dipping gently to the east-northeast with, in consequence, a regular succession of beds from west to east. Toward the Bermejo, in the western hills (an area not visited by us), are beds thought to be of Carboniferous and Permian age — the Paganzo beds of Bodenbender — followed by the Estratos de Ischichuca.[3] Farther east, the hills bordering the Ischigualasto valley are formed by the Estratos de los Rastros, dominantly sandstones, which conformably overlie the Ischichuca and include the coal seam and footprint locality mentioned. The shales occupying the valley constitute the Estratos de Ischigualasto, with a thickness estimated at 400 to 500 meters; it is in this formation that nearly all the vertebrate fossils of the region have been found. The steep cliffs at the east side of the valley constitute the lower part of the Estratos de Gualo of Frenguelli, for which Groeber and Stipanicic prefer the designation of Estratos de los Colorados. The four upper

[3] The beds beneath Cerro Morado may be the Ischichuca.

formations, at least, of the series — the Estratos de Ischichuca, de los Rastros, de Ischigualasto, de los Colorados — are obviously parts of a single sedimentary cycle, without evidence of any disconformity. In the region of Agua de la Peña a local fault (Frenguelli, 1948, pl. II, profile A) obscures the transition between los Rastros and Ischigualasto formations. But elsewhere (as Frenguelli's profiles B-D, pl. IV) deposition can be seen to have been uninterrupted, and (apart from a conglomerate bed which is taken as the upper boundary of the los Rastros formation) the transition is marked mainly by a diminution in importance of the sandstones which are so prominent in the los Rastros. The uppermost beds of the los Rastros yielded fragmentary vertebrate remains which appear comparable to those of the Ischigualasto formation. The typical beds of the Estratos de los Colorados contrast strongly with those of the Estratos de Ischigualasto in color, predominance of sandstones, and resistance to erosion; but as Frenguelli notes, a zone of transition is apparent at the base of the cliffs.

Stelzner "lumped" the entire series of beds found in this region as "Rhaetic" (in the broad sense in which that term has frequently been used in Argentinian geology). Bodenbender believed the "Gualo" beds to be Cretaceous, the Ischigualasto Jurassic, the los Rastros "Rhaetic." Frenguelli, more correctly, considers the series as a whole to be older, the "Gualo" to be Rhaetic or lower Liassic, the Ischigualasto to be upper Keuper, the los Rastros to be lower Keuper. Groeber and Stipanicic (table I) believe the spread in time of deposition of these beds to be rather narrower; the los Colorados are assigned with doubt to the Rhaetic, and both Ischigualasto and los Rastros to the upper Norian — i.e., the uppermost Keuper. The vertebrate remains suggest a lower position (Romer 1960a, pp. 1291-1292; 1960b, pp. 86-87) although full discussion should be postponed until the fauna has been more thoroughly studied. The Norian stage is one in which is found the typical Upper Triassic dinosaurian fauna; the Ischigualasto fauna is, on the contrary, one in which there is little evidence of dinosaurs and in which gomphodont cynodonts and rhynchosaurs are dominant. The Ischigualasto formation is essentially comparable to the Santa Maria beds of Brasil and the Manda beds of Tanganyika. It is surely pre-Norian and not improbably pre-Carnian; the gomphodont-rhynchosaur faunas would appear to be essentially Middle Triassic in age.

By agreement, the entire collection was shipped to Cambridge, where it is being prepared. All types and representative specimens of all forms found will be deposited in the National Museum in Buenos Aires. Complete preparation, however, will be a lengthy process, not only because of the considerable quantity of material but also because of the refractory nature of the matrix enclosing a large proportion of the specimens. In general, publication of the scientific results will not appear for some time, since we do not wish to publish before preparation has proceeded to the point at which all material of a given form has become available for study. In the case of the dicynodonts, however, the material included only a few specimens of a single large form; these have been prepared, and have been studied by Dr. Barry Cox, of King's College, University of London. A preliminary description is appended; it is hoped that a full account may be published within the year.

It is gratifying to us to have been instrumental in opening up a new Argentinian area for exploration by vertebrate workers. Since our trip, several further expeditions to the region have been made by the University of Tucuman, under the direction of Dr. Oswaldo Reig, with successful results; certain materials collected on these later expeditions have already been described (Reig 1958, Casamiguela 1960). There are vast areas of late Paleozoic and early Mesozoic deposits in the western Argentine which have never been visited by vertebrate paleontologists. Although the chances of finding beds as unusually productive as those of Ischigualasto are not great, it is highly probable that other faunas which will aid in rounding out the early history of vertebrates in Argentina await discovery.

I have elsewhere (Romer 1960a) expressed our thanks to a number of friends who aided us in the Mendoza region. We are further deeply grateful to various other persons who aided the general work of the expedition and our exploration of Ischigualasto. The cordial cooperation of Dr. Adolfo D. Holmberg, then Interventor, and members of the staff of the Buenos Aires Museum, was much appreciated. Professor Rosendo Pascual of the La Plata Museum accompanied us during the early portion of the trip. Much valuable scientific information was given us by the geologists of the Yacimientos Petrolíferos Fiscales, Comisión Nacional de Energía Atómica and the Dirección Nacional de Minería, including, among others, Drs. Pablo Groeber, Pedro N. Stipanicic, Martínez Cal, Héctor de la Mota, Luis A. Barrionuevo, and Vicente Ferreiro. The Comisión Nacional de Energía

Atómica aided us in the difficult matter of water and gasoline supply at Ischigualasto. Dr. Mario E. Terrugi aided us greatly in many regards, and the Harvard members of the expedition appreciate very much the hospitality extended to them by Dr. and Señora Terrugi and by the late Dr. Bernhard Dawson and Señora Dawson of La Plata. Our expedition was made possible by grants from the National Science Foundation and *Life* magazine.

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PRELIMINARY DIAGNOSIS OF *ISCHIGUALASTIA*, A NEW GENUS OF DICYNODONT FROM ARGENTINA

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Above is given a brief account of a joint Buenos Aires-Harvard expedition to the Valley of Ischigualasto, San Juan Province, Argentina. Among the remains collected from the Ischigualasto formation, presumably of Middle Triassic age, were several skulls and parts of posteranial skeletons belonging to a new genus of large dicynodont. A preliminary diagnosis of this new genus follows below; it is named *Ischigualastia jenseni* after Mr. James Jensen, who was responsible for the extremely painstaking collection and preparation of this material.

Ischigualastia jenseni, gen. et sp. nov.

Holotype of I. jenseni: Number 18.055, Muséo Argentino de Ciencias Naturales, consisting of skull and partial skeleton.

Geological Horizon and Locality: Ischigualasto formation (Triassic), approximately 100 m. above the base of the formation; about 2 km. north of Agua de la Peña, Ischigualasto Valley, Department of Valle Fertíl, San Juan Province, Argentina.

Genotype: Ischigualastia jenseni Cox.

Generic and Specific Diagnosis: Large dicynodont (type skull 55 cms. long, 46 cms. broad). No teeth in upper or lower jaws. Skull triangular in dorsal view, greatest width across occiput. Very wide interorbital region, very narrow intertemporal region. Tapering snout, without nasal ridges or bosses. No pineal boss, but a slight mound in front of pineal foramen. No postfrontal bone. Preparietal bone probably present. Interparietal forms whole of posterior half of intertemporal bar, widely separating squamosals from postorbitals. No sharp median intertemporal ridge. Zygomatic arches bowed outward. Sharp transition between dorsal and occipital surfaces. Occiput almost semicircular in outline. No tabular bone visible. Stapes lacks stapedial foramen. Short interpterygoid vacuity. No ectopterygoid bone. Pterygoid broadly meets maxilla. Palatine and premaxilla meet, excluding maxilla from internal nares. Palatal surface of premaxilla bears pair of anterior ridges. Premaxilla

extends some way anterior to maxilla. Ascending portion of epipterygoid slender, not expanded to form part of lateral wall of braincase. No lateral wing on dentary. Stout retro-articular process.

Five sacral ribs. Acromion process of scapula absent or vestigial. Coracoid foramen between precoracoid and scapula. Sternum constricted halfway along its length; dorsal surface bears bosses for attachment of ribs. Ulna has large olecranon process, with cartilaginous epiphysial union with rest of bone. Femur with well-developed head set off from rest of bone.

A more extensive and illustrated account of *Ischigualastia* will appear later.

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A RHACHITOMOUS AMPHIBIAN, *SPATHICEPHALUS*, FROM THE MISSISSIPPIAN OF NOVA SCOTIA

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In the past few years field parties from the Museum of Comparative Zoology at Harvard College, supported in part by funds from the National Science Foundation, have discovered several deposits of fossil amphibians which date from the earlier half of the Carboniferous period. Most of the material recovered comes from redbeds of the Upper Mississippian Mauch Chunk group in West Virginia (Romer, 1941) and Pennsylvania; more recently, amphibians have been found in beds of equivalent age at two sites in Nova Scotia.

In continuation of the Harvard collecting program, field parties sponsored jointly by Princeton University and the Nova Scotia Museum of Science have collected additional bones and trackways of amphibians in Pennsylvanian as well as Mississippian beds. One of these finds is noteworthy because no member of the order Temnospondyli from the Mississippian system has hitherto been described.

This specimen, the right half of a skull table preserved as a natural mold, comes from the same horizon and locality as the embolomerous lower jaw described as *Pholiderpeton*(?) *bretonense* Romer (1958). The matrix is a flaggy calcareous siltstone characterized by well-sorted quartz grains and silvery muscovite mica.

Superorder Labyrinthodontia

Order Temnospondyli

Suborder RHACHITOMI[1]

Family LOXOMMIDAE

Genus Spathicephalus Watson 1929

[*Spathiocephalus* Romer 1945, *errore*]

Emended Diagnosis. A loxommid extremely specialized in its expanded cheek and snout, constricted interorbital area and shortened skull table, and having numerous small, chisel-shaped marginal teeth.

Spathicephalus pereger, n. sp.

Diagnosis. Differs from *S. mirus* Watson, the only other known species, in its relatively narrower skull table.

Type. PU 17182, Princeton University Geological Museum.

Occurrence. Point Edward formation, Canso group, Upper Mississippian (probably early Namurian). Beach of cove between Point Edward and Keating Cove, 4 miles northwest of Sydney, Cape Breton County, Nova Scotia. Collected by Donald Baird, William F. Take and Jane McN. Take, 1960.

DESCRIPTION

The dorsal surface of the skull table bears a deep, coarsely reticular sculpture rather similar to that of *Megalocephalus lineolatus* (Cope) but with narrower ridges. Aside from the separation of prefrontal from postfrontal, the contacts between skull elements are normal for a loxommid.

The narrow frontal bone is bounded medially by a deep, straight suture which is ridged rather like the edge of a file. Anteriorly the frontal is beveled to receive the end of the nasal; anterolaterally it bears a long, striated facet for the articulation of the prefrontal. As in other loxommids the prefrontal must have swelled laterally to form the antorbital process which dif-

[1] Assignment of the Loxommidae to the Rhachitomi is now confirmed by the association of rhachitomous vertebrae with a skull of *Megalocephalus lineolatus* (Cope) from Linton, Ohio (cf. Baird, 1957).

ferentiates the orbit proper from its anterior extension, the lacrimal fenestra, and gives the loxommid eye-socket its characteristic keyhole shape. Most of the lateral edge of the frontal forms the thick orbital rim. At its waist the frontal is 4.3 mm. wide, making the interorbital distance a mere 8.6 mm. — extraordinarily narrow for a skull with an estimated width of 185 mm.

The short parietal extends laterally into a square lappet; there is no indication that this lappet represents a former intertem-

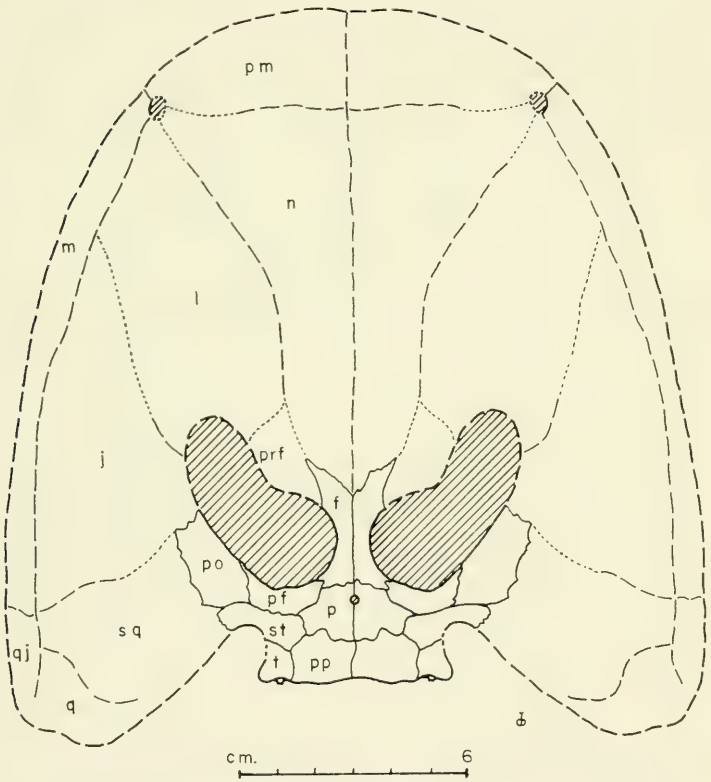

Fig. 1. Skull of *Spathicephalus pereger*, n. sp., x ½. Restoration in dashed lines based on *S. mirus;* dotted lines conjectural. Abbreviations: *f*, frontal; *j*, jugal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *p*, parietal; *pf*, postfrontal; *pm*, premaxilla; *po*, postorbital; *pp*, postparietal; *prf*, prefrontal; *q*, quadrate; *qj*, quadratojugal; *sq*, squamosal; *st*, supratemporal; *t*, tabular.

poral element. Centered in the anterior half of the inter-parietal suture lies the parietal foramen, 2.3 mm. in diameter, which housed the parapineal eye. The postparietal (dermal supraoccipital) is relatively large.

A thin oval lamina slopes outward from the corner of the tabular. Ventromedial to this flange lies the backward-jutting tubercle which is characteristic of loxommid tabulars but which also occurs in such genera as *Edops* (Romer and Witter, 1942). Whether this process is a true homolog of the tabular horn in other labyrinthodonts and perhaps of the tabular lamina in *Acanthostega* remains to be determined. Unfortunately, the lateral margins of the tabular and supratemporal are not clearly defined in the specimen. The greatly broadened supratemporal, however, is evidently embayed by the apex of the otic notch — a condition also found in *Baphetes* and *Megalocephalus brevicornis* [*Orthosaurus pachycephalus* of Watson, 1926].

The postfrontal, which in most labyrinthodonts lies posteromedial to the orbit, here lies directly posterior to it. In consequence the postorbital has been thrust outward onto the cheek along with most of the supratemporal; its orbital margin is 19 mm. long and nearly straight. In its new orientation the postorbital might be called exceptionally long rather than exceptionally broad.

Watson's (1929, fig. 22) illustration of the skull of *Spathicephalus mirus*, scaled to the interorbital width and post-orbital length of *S. pereger*, forms the basis for the reconstruction in Figure 1. The restored skull of *S. pereger* measures 177 mm. in mid-sagittal length as compared to 198 mm. for the type skull of *S. mirus*. As nothing is known of the posteranial skeleton in this genus, the dimensions of the whole animal cannot be estimated.

COMPARISON

Inconsistencies between the Point Edward specimen and the published account of *Spathicephalus mirus* might be interpreted as generic distinctions. Many of the discrepancies, however, can be attributed to differences in the manner and quality of preservation. For example, the suture pattern illustrated by Watson is that of the ventral surface of the skull roof and can be expected to differ somewhat from that of the dorsal surface.

The single element labeled "postorbital" in Watson's figure of *S. mirus* occupies the position of the postfrontal and half of the postorbital in *S. pereger*. Since the suture between jugal and squamosal meets the outer corner of this element — as it does the corner of the postorbital in all known loxommids — Watson's identification must be correct. If (as he suggests) the postfrontal forms part of the undifferentiated interorbital bar in *S. mirus*, then the two species differ markedly in this respect. Watson illustrates a suture which bisects the antorbital process at right angles to the lateral margin of the nasal bone, and interprets this suture as separating the lacrimal from a wing of the interorbital bar. New evidence now permits a more conventional reconstruction of this region. No parietal foramen was observed in the Scottish material, but a foramen of normal size and position is evident in the Nova Scotian specimen.

One clear distinction lies in the relatively narrower skull table of the new species: in *S. mirus* the ratio of interorbital width to table width is 1:7 while in *S. pereger* it is 1:6. Another difference is that even when allowance is made for post-mortem distortion of the cheek region, the orbits seem to have been more obliquely placed in *S. pereger* than in *S. mirus*.

DERIVATION OF *SPATHICEPHALUS*

Grotesquely modified though it is, the skull structure of *Spathicephalus* (as elucidated by the new specimen) can be readily derived from that of more typical loxommids. As it happens, one species which can be said to represent a pre-*Spathicephalus* morphological stage is also the only older loxommid known: *Loxomma allmanni* Huxley from the Gilmerton ironstone of Scotland. The Lower Limestone group in which it was found directly underlies the Limestone Coal group in which *Spathicephalus mirus* occurs.

In the transition between the morphological stages represented by *Loxomma* and *Spathicephalus*, posteromedial migration of the orbits has displaced the supraorbital elements so that the frontal bone forms much of the orbital rim — a condition repeated in various genera of labyrinthodonts but more commonly associated with enlarged orbits. Concomitantly the cheek and snout have broadened and flattened into a condition which recalls the early Permian zatracheids *Acanthostoma* and *Zatrachys*. The constriction of the frontals into a narrow bar, together with the

shortening of the skull table, loss of the intertemporal bone and lateral displacement of the postorbital and supratemporal, are unexpected extremes of specialization in so early a genus. Such a condition did not recur, so far as we know, until the development of the plagiosaurs in late Triassic time (cf. Panchen, 1959, fig. 16).

The specializations of *Spathicephalus* evidently adapted it to life as a bottom-dwelling fish-eater. Among labyrinthodonts of this ecotype — e.g. *Erpetosaurus, Zatrachys, Capitosaurus, Eupelor* [*Buettneria*], *Gerrothorax* — the lower jaw articulation tends to be aligned with the occipital condyle, so that the mouth could be opened by raising the snout while the thorax remained prone on the bottom (cf. Watson, 1951, pp. 67-70). A similar tendency is evident in *Spathicephalus*, for its occipital and quadrate condyles are more nearly aligned than those of any other loxommid except the late Westphalian species of *Megalocephalus*.

Surely the extent of modification which *Spathicephalus* had achieved by late Mississippian time presupposes a long previous history — yet to be revealed — for the Loxommidae.

ASSOCIATED FAUNA

A *Gyracanthus* spine, a supposed *Sagenodus* quadrate and fragmentary fish remains were found in the flagstone layer with the mandible of *Pholiderpeton*(?) *bretonense* in 1956. From this same layer the 1960 field party collected the type of *Spathicephalus peregor* and the proximal third of another *Gyracanthus* spine (PU 17185).

About 12 feet lower in the section, bones coated with red iron oxide occur in an 18-inch zone of highly calcareous mudstone, rich in ostracodes and *Spirorbis*, which is intercalated with layers of limey shale. A *Gyracanthus* spine (PU 17186), a skull bone of the lungfish *Sagenodus* (the left "E" plate, PU 17187), and scales and scrap of the crossopterygians *Megalichthys* and *Strepsodus* (PU 17188, 17189) represent a typical assemblage of Carboniferous fresh-water fishes. Amphibian remains from this horizon include a left clavicle, a phalanx and a ventral scale (PU 17190), all apparently embolomerous.

STRATIGRAPHY

The Point Edward formation is assigned to the lower part of the Canso group. While the Canso cannot yet be correlated precisely with European and other American sequences, it appears

on the basis of fossil floras (Bell, 1944, pp. 23-24) and invertebrates (Copeland, 1957, pp. 6-8) to be more or less equivalent stratigraphically to the Lower Namurian of Europe. Since in current practice the lower boundary of the Upper Carboniferous system coincides with that of the Namurian, the Point Edward formation is classified in European terms as basal Upper Carboniferous. In North America, however, the Carboniferous is subdivided differently: its upper half constitutes the Pennsylvanian system which includes equivalents of the Upper but not the Lower Namurian. Thus the Point Edward formation is classified in American terms as Upper Mississippian (Weller et al., 1948).

The Scottish specimens of *Spathicephalus* were found in the Loanhead No. 2 ironstone of the Midlothian coalfield, a bed which lies in the upper half of the Limestone Coal group (Tulloch and Walton, 1958). This group is believed to be approximately equivalent to Goniatite Zone E_1 (characterized by *Eumorphoceras*) and the lower part of Brachiopod-Coral Zone D_3 (characterized by *Dibunophyllum*); these zones correspond to the Lower Namurian of continental Europe (Trueman, 1954). At the risk of confusion it should be added that although the Eumorphoceras Zone forms the base of the Upper Carboniferous, the flora and the fish fauna of this zone show Lower Carboniferous affinities and are separated from their Upper Carboniferous counterparts by a distinct biotic break. The sequence of amphibian-bearing beds in the Scottish Carboniferous has been reviewed by Westoll (1951) and most recently by Panchen and Walker (1961).

In summary, although the correlations involved are still rather tentative on both sides of the Atlantic, current stratigraphic practice assigns an early Namurian age to both the Scottish and Nova Scotian species of *Spathicephalus*. The epoch in which they lived was evidently one of biotic transition between the earlier and later phases of the Carboniferous.

In view of the stratigraphers' uncertainty, the possible utility of *Spathicephalus* as an index fossil is worth investigating. For the most part the loxommid amphibians are too imperfectly known for their distribution to be stratigraphically significant. The best-known genus, *Megalocephalus* [*Orthosaurus*], ranges through early and middle Pennsylvanian time, i.e. from Westphalian substage A to late Westphalian D (Panchen and Walker, 1961; Baird, 1957). But since *Spathicephalus* is the most extremely specialized member of the family it may have existed over a comparatively short span of geologic time.

SUMMARY

A partial skull roof of the loxommid labyrinthodont *Spathicephalus*, previously known only from the Limestone Coal group of Scotland, has been found in the Point Edward formation of the Canso group near Sydney, Nova Scotia. The suture pattern (hitherto incompletely known) of this extremely specialized genus is described and derived from that of more typical loxommids. *Spathicephalus*-bearing beds of Scotland and Nova Scotia are considered to be early Namurian in age, corresponding to the base of the Upper Carboniferous in Europe and the top of the Mississippian system in North America. *S. peregeri* n. sp. is the first-described temnospondylous amphibian of Mississippian age from the Western Hemisphere.

ACKNOWLEDGEMENTS

This study owes much to the hospitality and cooperation of Director Donald K. Crowdis and staff members William F. and Jane McNeill Take of the Nova Scotia Museum of Science in Halifax. F. B. Van Houten analyzed the source rock; A. L. Panchen provided most helpful advice on matters of British stratigraphy; Edward S. Belt has generously shared the results of his current research on Canso stratigraphy and sedimentation. Financial support from the William Berryman Scott Research Fund of Princeton University (administered by Glenn L. Jepsen) and the National Science Foundation made possible the field work.

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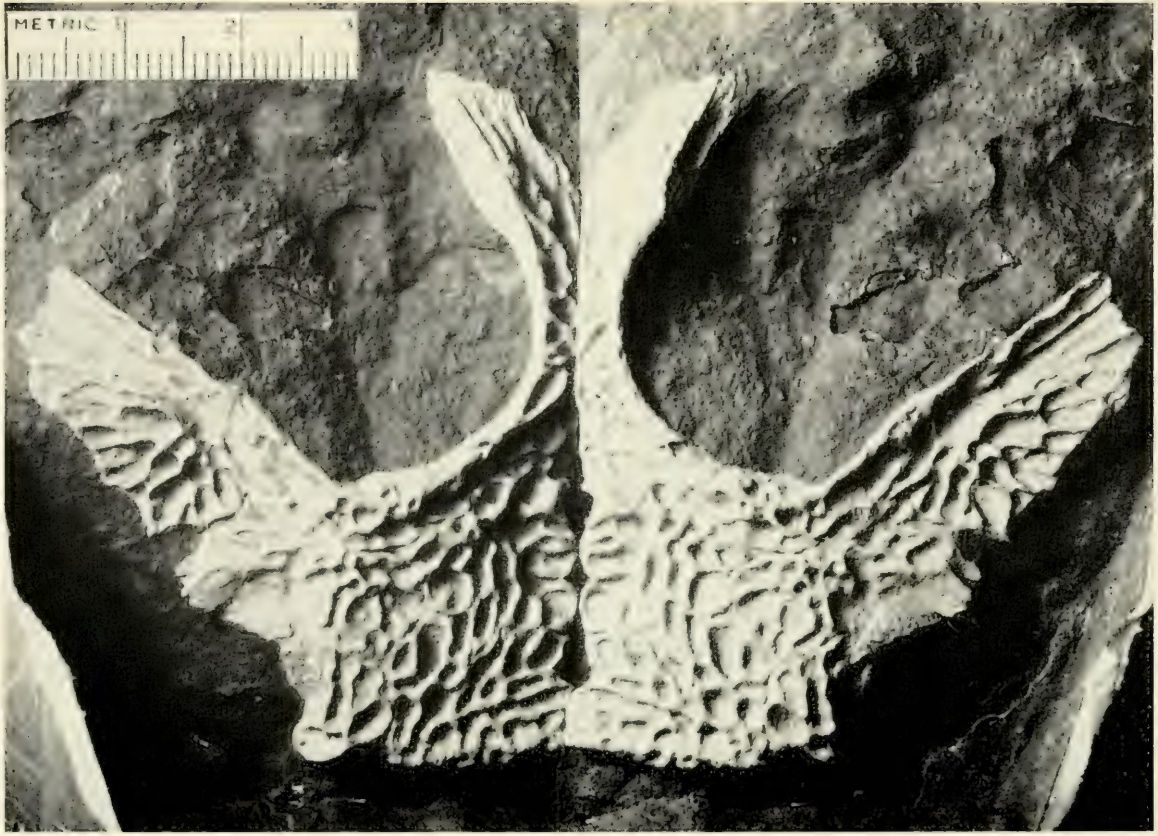

Skull table of *Spathicephalus peregeri*, n. sp., from a bicolored latex cast. Left half restored from a photograph which has been illuminated and printed in reverse.

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. MAY 29, 1962 NUMBER 158

A FOSSIL GERRHOSAUR FROM THE MIOCENE OF KENYA (REPTILIA: CORDYLIDAE)

BY RICHARD ESTES[1]

Many thousands of fossils, both plant and animal, have been collected since 1947 in the Kavirondo Gulf area, Lake Victoria, Kenya. Most of these fossils come from sediments on Rusinga and Mfanganu Islands, within the Gulf. The vertebrate fauna is diverse, though principally mammalian; thus the discovery of the fossil lizard described here is of special interest. Much of the fossil mammalian fauna has been described in a British Museum of Natural History series (see e.g. LeGros Clark and Leakey, 1951; Whitworth, 1958). Part of the extensive seed-nut flora has recently been described by Chesters (1957). Leakey (1952) has noted and figured some of the remarkably well-preserved invertebrates.

The age of the fossils in this sequence has been assigned entirely on faunal grounds, and is usually considered to be early Miocene (Burdigalian). The reasons for this age determination are given in the papers mentioned above. The presence of both archaic and modern elements in the mammalian fauna as well as our lack of knowledge of the Cenozoic sequence in tropical areas make it difficult to assign a firm date to these deposits. Suggestions ranging from Oligocene to "considerably younger than the lower Miocene" (LeGros Clark and Leakey, 1951) have prompted Whitworth (1958, p. 45) to state that "it is clear that the question of geological age may have to be revised when the description of the East African fossils is completed."

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Class Reptilia

Order Sauria

Family CORDYLIDAE

Subfamily GERRHOSAURINAE

Gerrhosaurus cf. G. major Duméril

Referred specimen. — Coryndon Museum, Nairobi, M. F. W. 1955/1.

Locality. — Mfanganu Island, Lake Victoria, Kenya, Africa. Area B, of Red Earth Series as mapped by Whitworth (1953). An extensive flora and invertebrate fauna have also been collected from these deposits, but have not yet been described.

Age. — Early Miocene (Burdigalian?).

Preservation and major features of the specimen. — As preserved, the total length of the specimen is 55 millimeters. It consists of most of the head and the greater part of the neck, though it is probable that much more if not all of the entire body was originally present. The external features, many of them from the soft anatomy, are in part completely replaced with calcite. Some bone is preserved internally, but selective replacement has occurred. The external calcite covering is about 3 or 4 millimeters thick, and internal to this the neck and posterior skull region are filled with a soft waxy black sediment which contains small calcite crystals. No trace of the posterior bones of the skull is visible. The head is slightly twisted to the left, and the half-open mouth is filled with calcite. A striking feature of this specimen is the replacement of the tongue by calcite, though no important details of structure are visible. Dorsally, especially in the neck and posterior skull region, the specimen is heavily crushed; otherwise, there is little distortion. The shape of the depression in the top of the skull, the half-open mouth, and lack of crushing in the facial segment suggest that the animal may have been stepped on, perhaps by the sharp hoof of a grazing animal. This might have caused the animal's death, or could also have happened shortly after it was buried by sediment.

The palatal, facial, and marginal bones of the snout are broken or missing. Most of the teeth are eroded, though their outlines are preserved as imprints in the calcite filling of the mouth, but in some places a few tooth crowns still remain, as well as fragments of tooth shafts.

The eye sockets are completely filled with calcite, though the right one is badly eroded. On the left side, the calcite has taken an impression of the underside of the supraorbital plates, but their number cannot be determined. One of the most unusual features of this specimen is the preservation of the external shape of the left eye, in calcite. The lids are sharply delineated, and between them, a low, domed area reflects the outline of the cornea or perhaps the underlying lens.

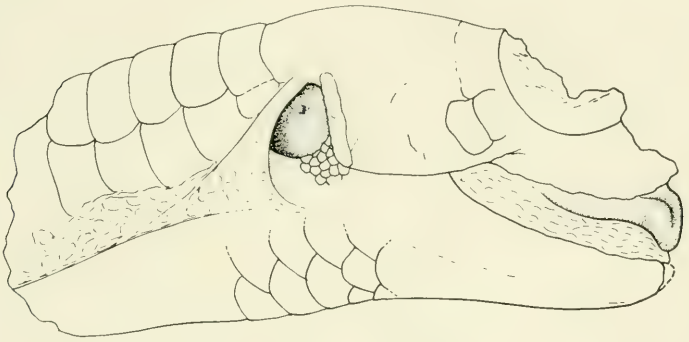

Fig. 1. *Gerrhosaurus* cf. *G. major*, Lower Miocene, Kenya, right lateral view, x 1.5.

The outline of the outer ear and tympanum is perfectly preserved on the right side, though on the left much of it is broken away. The anteroposterior diameter of the ear opening is less on the left as a result of twisting of the head. Many of the granular scales which surround the ear region and extend into the lateral fold are clearly visible. The tip of the extracolumella is strongly imprinted on the tympanum. The lateral fold is prominent on both sides, but is especially clear on the right, where it has been stretched open by twisting of the body on the median axis before deposition.

Very little remains of the posterior skull bones. A thin film of prefrontal and palatine surrounds the left eye, and directly below, small portions of the vomers protrude. Maxillae and dentaries are badly broken, and little remains other than thin edges of their internal processes. Under both eyes parts of the internal faces of the jugals are visible as imprints.

Dorsally, there are imprints of seven or eight postcranial scale rows. They end anteriorly near a smooth flat surface which

represents the skull roof, but whatever bone or scale imprints may have been preserved are no longer present.

Description. — The large imbricate osteoscutes of the throat region are compound; each is formed of multiple polygonal or trapezoidal osteoderms. The anterior ones are small, smooth, and subequal, the posterior ones elongated and either smooth or faintly wrinkled. The posterior borders of the osteoscutes are rounded or slightly squared. The throat osteoscutes are in seven longitudinal rows between the lateral folds, and they alternate rather than being aligned in straight transverse rows. Posteriorly, their arrangement is somewhat distorted as a result of post-mortem dislocation of some of the scales. Two pairs of large non-imbricate chin shields seem to have been present, formed of small subequal polygonal osteoderms.

The lateral folds appear to have contained small or granular scales, but this is uncertain. Both folds extend as far forward as the ear.

The subtriangular outer ear opening is covered ventrally with small squarish or lenticular scales which grade into those of the lateral fold. On the posterior border of the ear opening, several marginal rows of small scales are followed by a row of slightly larger ones. The tympanic shield is strap-shaped, narrow, and not at all posteriorly expanded.

The dorsal scales of the neck, of which imprints of seven or eight straight transverse rows are preserved behind the occipital margin, are large and subrectangular.

Abrasion has removed almost all imprints of scales from the cheek, but a few large ones are visible anteriorly.

The pleurodont teeth are robust, tall, and columnar. Imprints of their closely-spaced shafts indicate that replacement teeth were formed in subcircular basal excavations. Preserved tooth crowns are faintly tricuspid.

Discussion. — Union of the gerrhosaurs and cordylines as subfamilies of the Cordylidae, as recently suggested by McDowell and Bogert (1954), is undoubtedly correct. The presence of compound osteoderms in cordylines (*sensu stricto*), a character not mentioned by these authors, further emphasizes the separation of this group from the anguimorphs and allies them with the scincomorphs.

Until now, the cordylids have had no clear fossil record. *Pseudolacerta mucronata* (Filhol) has been tentatively placed in this family by Romer (1956, p. 552). De Stefano (1903, p. 413)

and Filhol (1877, p. 489) do not mention any characters of taxonomic value, and Filhol's illustration (*ibid.*, fig. 423) is vague and diagrammatic. Hoffstetter (1944, p. 553) considers it possibly a skink, but notes that vertebrae similar to those of *Cordylus* (*sensu latu*) occur in the same deposit. Later, he indicates (1955, p. 621) that these fossils "rappellent les pièces homologiques de l'actuel *Cordylus*," but the assignment is still tentative.

The fossil described here is referable to the subfamily Gerrhosaurinae on the basis of the large, broadly imbricate, rounded or slightly squared throat scales, contrasting with the much smaller, non-imbricate, diamond-shaped throat scales of the cordylines. *Chamaesaura* has larger throat scales than other cordylines, but they are anteroposteriorly elongate and mucronate, rather than smooth and transversely widened as in gerrhosaurines.

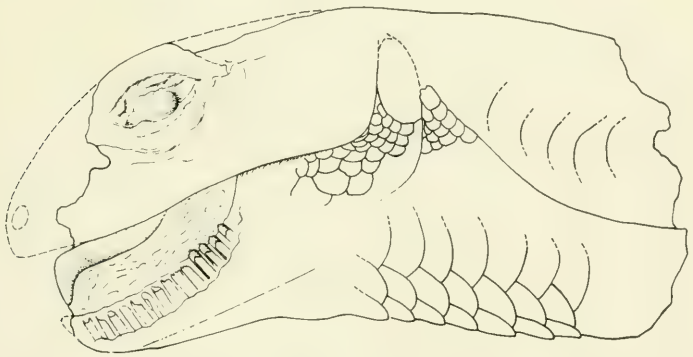

Fig. 2. *Gerrhosaurus* cf. *G. major*, Lower Miocene, Kenya, left lateral view, x 1.5.

Though the published generic characters of *Gerrhosaurus* are in soft anatomy and scale details not preserved here (Loveridge, 1942, p. 488; FitzSimons, 1943, p. 268), similarity between this fossil and Recent members of the genus seems to indicate that it belongs here. The throat scales, what remains of the dorsal scales, shape of the ear and lateral fold all agree closely with these characters of the Recent genus. Moreover, a number of resemblances discussed below strongly suggest reference to the Recent species *G. major*.

1. The fossil has the size and general proportions of a large adult individual of *G. major*. The latter is the largest of the species of *Gerrhosaurus;* most other species are considerably smaller.

2. The shape of the opening of the external ear in *G. major* may be rounded or slightly angular dorsally. In the available specimens, *G. m. major* most frequently shows the rounded condition, but *G. m. grandis* usually has a more angular dorsal edge, as in the fossil. *G. m. bottegoi* resembles *G. m. major* in this character.

3. In gerrhosaurs, the shape of the tympanic shield is considered taxonomically significant. This scale lies on the anterior border of the outer ear, and in all species of *Gerrhosaurus* except *G. major*, is thin, flattened, and often expanded to cover and protect the cavity of the outer ear (see e.g. FitzSimons, 1943, figs. 150, 156). Loveridge (1942, pp. 515, 518) states that tympanic shields of *G. flavigularis* are also narrow and band-like as in *G. major*. This is grossly true, but in detail the two can be distinguished easily. *G. flavigularis* has a narrowly crescent-shaped tympanic shield (see e.g. FitzSimons, *ibid.*, fig. 154; cf. fig. 164 of *G. m. grandis*) which is thin and flattened, while that of *G. major* is strap-shaped, and thickened.

4. Another similarity to *G. m. grandis* is the presence, on the posterior border of the outer ear opening, of a small anterior row of scales, flanked by a larger posterior row. In *G. m. major* and *G. m. bottegoi* these scales tend to be subequal. This character varies somewhat, and in any case the time separation as well as lack of further preserved characters precludes reference of this fossil to one of the living subspecies. However, this character and that given as number 2 above seem to suggest a closer relationship to *G. m. grandis* and *G. m. bottegoi* than to *G. m. major*. The other subspecies, *G. m. zechi*, is known from only a few specimens, none of which were available to me. It is very closely related to *G. m. bottegoi* and its status is not clear at this time.

Distribution of Recent *Gerrhosaurus major*

G. major occurs today in principally arid savanna along the eastern coast of Africa, north to Eritrea and south to Zululand. *G. m. grandis*, the most southern subspecies, is found from Zululand north to Morogoro, Tanganyika. *G. m. major* is a coastal

subspecies, principally in Tanganyika, but reaching as far north as Kenya. *G. m. bottegoi* ranges from central Tanganyika north through central Kenya and reaches north to coastal Eritrea, farther north than any other gerrhosaur, and is the only subspecies of *G. major* found today in the Kavirondo Gulf region of Lake Victoria, the same region as the occurrence of the fossil. The problematical *G. m. zechi* has, so far as known, a disjunct distribution limited to the northern Belgian Congo and Togo.

CONCLUSIONS

The fossil described here is closely related to, and perhaps conspecific with, the Recent species *Gerrhosaurus major*. Thus it is extremely probable that the habitat of the lizards represented by the fossil was semi-arid or arid savanna, like that of the modern species. The presence of a mammalian fauna of

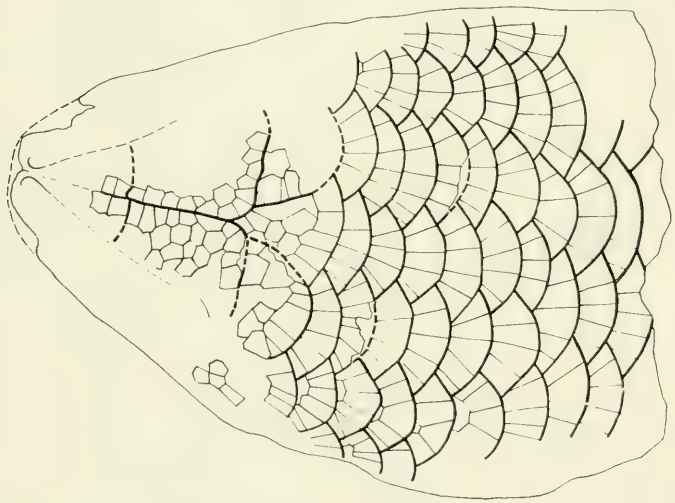

Fig. 3. *Gerrhosaurus* cf. *G. major*, Lower Miocene, Kenya, ventral view, x 1.5.

dominantly savanna aspect in these deposits supports this conclusion. Whitworth (1953, p. 82) states that ephemeral lakes were probably present in this region in the late Miocene, allowing the savanna mammals access during the periods of desiccation indicated by the sediments. He also points out that similar

situations occur today in areas of the northwestern Sudan. Chesters (1957), on the basis of the flora, has concluded that a "gallery-type forest in which trees festooned with climbers overhung the watercourses" lived near to the site of deposition, and that many of the fossil nuts and seeds represent living tropical African genera.

Close relationship of the fossil with the Recent species indicates that at least part of the pattern of speciation seen within the genus today is of considerable antiquity. Moreover, similarities of the fossil to some of the Recent subspecies of *G. major* perhaps indicate that some of the geographic variants seen today were beginning to appear, as far back as the Miocene. The two Recent subspecies which the fossil most closely resembles, *G. m. bottegoi* and *G. m. grandis*, are northern and southern populations which intergrade in the area immediately south and east of Lake Victoria. It is interesting, but highly speculative, to suggest that the occurrence of the fossil near the present area of intergradation of these two Recent subspecies might either indicate a stage in the development of the Recent subspecific patterns, or an intergrade between the two which could possibly be duplicated today if sufficient specimens were available.

Moreau (1951, esp. pp. 877, 881) has gathered evidence which suggests that at least from the mid-Cenozoic to the present, central and eastern Africa had a climate and broadly defined vegetational types which differed relatively little from those occurring there today. If this is so, the above alternatives are quite possible, yet additional fossil evidence, both biotic and climatic, is necessary to accept or reject either of them.

SUMMARY

The well-preserved head of a fossil lizard from the Lower Miocene (Burdigalian?) of Mfanganu Island, Lake Victoria, Kenya, is tentatively referred to the Recent species *Gerrhosaurus major* (Reptilia: Cordylidae). Many external features of soft anatomy are preserved as casts in calcite, including the eye, tongue, and tympanic membrane. Close relationship to the Recent semi-arid or arid savanna species indicates a similar habitat for the fossil, a conclusion corroborated by the savanna aspect of the fossil mammals from contemporaneous deposits on nearby Rusinga Island. This specimen is one of the oldest vertebrate fossils even tentatively referred to a Recent species and must indicate that at least part of the pattern of speciation seen in Recent gerrhosaurs is of relatively ancient origin.

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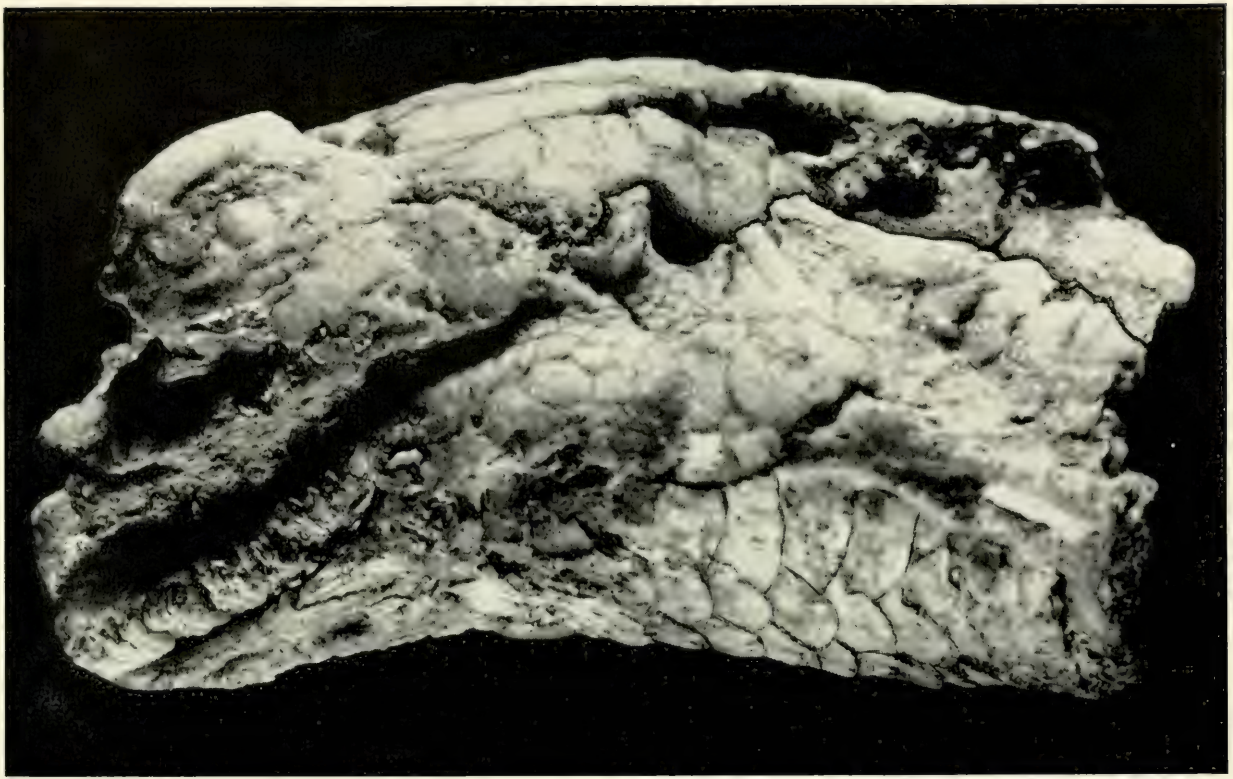

Plate 1

Gerrhosaurus cf. *G. major*. Photograph of left lateral view. Skull crushed dorsally. Note especially outline of eyelids and cornea, slightly protruding tongue, and well-preserved scale outlines. Not to scale. Slightly retouched. Photograph by Frederick Maynard, Boston University.

BREVIORA

Museum of Comparative Zoology

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AGE IN A SMALL SAMPLE OF BLUEFISH (*POMATOMUS SALTATRIX* (LINNAEUS))[1]

By RICHARD H. BACKUS

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Little is known about the life-history of the bluefish (*Pomatomus saltatrix*) even though this long-known species is widely distributed in warm and temperate seas and is valuable for food and sport. Not only have the eggs and larval young of this interesting fish not been positively identified, but nothing exact is known of its rate of growth although the "annuli" on its scales prove to be quite easily read. Perhaps it is the great population fluctuations of this fish and its erratic appearance in many waters which have discouraged naturalists from studying it. Bigelow and Schroeder (1953) give a summary of what is known of bluefish life history. Little has been added since their account was written.

To learn something of the growth of the species, advantage was taken of the abundance of bluefish around Woods Hole during the autumn of 1961 and of the angling expertness of Asa Wing, Henry Cain, and Carl Grant, Jr. These men saved heads and scale samples together with records of fork length from the 34 fish that they caught between October 9 and 19 in Great Harbor at Woods Hole, in Woods Hole passage, and along the east shore of Buzzards Bay north of Woods Hole.

The saccular otolith of the bluefish has been figured by Le Gall (1934) and by Sanz Echeverría (1950). Le Gall (*op. cit.*) also figured the scales, and in another paper (1935) he said that his examination of the scales in North African specimens suggests that "young individuals attain their adult size and their first sexual maturity at the age of 4 or 5 years." On the other hand,

[1] Woods Hole Oceanographic Institution Contribution No. 1234

Borcea (1936) says of Black Sea bluefish: "During the second year they reach dimensions of 14-20 cm and can attain the first sexual maturity."

TABLE 1

Fork length and age in a small sample of bluefish.

Fork Length (inches)	Age (annuli)	Fork Length (inches)	Age (annuli)
13.9	I+	15.2	I+
14.0	I+	15.2	I+
14.0	I+	15.5	I+
14.0	I+	15.5	I+
14.0	? (I+ or II+)	15.5	I+
14.1	? (I+ or II+)	15.5	II+
14.1	I+	15.8	I+
14.2	I+	16.0	I+
14.2	I+	16.2	II+
14.4	I+	16.5	I+
14.5	I+	17.0	II+
14.5	I+	17.5	II+
14.8	I+	18.0	II+
15.0	I+	19.0	II+
15.0	II+	19.0	II+
15.0	? (I+ or II+)	20.1	II+
15.1	I+	24.0	III+

An otolith extracted from a specimen in our sample 14.4 inches in fork length measured about 0.45 by 0.15 inches. The otolith is much sculptured and does not seem suitable for use in age determination by simple visual inspection though it might be so suited if x-ray methods were used. Since the scales of this fish are large, and those examined by us seem to show the annuli rather clearly (Figure 1), we have relied on the scales alone for the ages reported here.

Fork length and age for the specimens in our sample are given in Table 1. Fork lengths were taken to the nearest eighth of an inch, were converted to decimals and rounded to the nearest tenth. Ages (expressed in annuli) were determined by examining at least 10 legible scales from each specimen. In three cases consistent results could not be obtained. Thus, age has been determined with some confidence in 31 instances. Of these, 21 specimens show an age of I+, nine an age of II+, and one an age of

III+. Specimens of age I+ range from 13.9 to 16.5 inches in fork length and have a mean length of 14.85 inches. Specimens of age II+ range from 15.0 to 20.1 inches and have a mean length of 17.48 inches. The sole III+ specimen measures 24.0 inches in fork length. Because of the small size of our sample these data can do little more than show that snappers (as small bluefish are called) of four to nine inches, seen in the autumn (Bigelow and Schroeder, 1953), are indeed young of the year and that such fish approximately double their length in the succeeding 12 months.

Bluefish left the Woods Hole area during the course of a five-day northeast storm which commenced on the evening of October 19 and lasted until the early hours of October 25. The last fish in our sample was caught on October 19. None were caught after the passage of the storm although the fishing effort continued and produced good catches of striped bass (*Roccus saxatilis*). Surface temperature records for Great Harbor, Woods Hole, show fluctuations between 64.9 and 64.5°F for the period October 6 to 12, a decline from 64.5 to 60.8°F from October 12 to October 19, the day the storm began, a decline from 60.8 to 55.0°F during the storm, and small fluctuations about 55°F for the remainder of the month. One may suppose that at about 60°F the bluefish were near the minimum temperature that they can tolerate at this stage of the life cycle and that the catastrophe of the storm, with the accompanying further drop in temperature, was enough to start them on the journey to their winter haunts.

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FIG. 1. Scale from a bluefish (*Pomatomus saltatrix*) 20.1 inches in fork length taken in Woods Hole passage on October 17, 1961, showing two annuli.

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. JUNE 12, 1962 NUMBER 160

TWO NEW ARTHROPOD CARAPACES FROM THE BURGESS SHALE (MIDDLE CAMBRIAN) OF CANADA

BY W. D. IAN ROLFE

Three carapaces of an undescribed arthropod were found by the writer when curating the large Museum of Comparative Zoology collection of Burgess Shale arthropods, collected by P. E. Raymond, H. C. Stetson, W. E. Schevill and C. H. Burgess in August, 1930. Subsequent search through the material in the U. S. National Museum, Washington, D. C., yielded eleven further specimens and two specimens of another new form, which had been set aside for description by C. E. Resser. The writer is indebted to Dr. G. A. Cooper for permission to borrow and describe the U.S.N.M. material and to Dr. H. B. Whittington for the photographs and for criticism of the manuscript.

The USNM specimens came from Walcott's quarry at locality 35k near Field, British Columbia (Walcott, 1911, pp. 51-52; Resser, 1929, p. 2; = locality S11f of Rasetti, 1951, pp. 37-38, 103, 129). The MCZ specimens were also probably collected from this quarry, although it is impossible to be certain of this since the 1930 expedition also collected from "a second layer . . . very fossiliferous . . . some seventy feet further up the mountainside" (Raymond, 1930, p. 32; 1935, p. 205). This second locality possibly corresponds with Rasetti's S11g (1951, pp. 38, 104, 130) and details of the stratigraphy of these two horizons are given in that work. Letters a and b following a specimen number indicate that part and counterpart are present.

Carapace shape alone is insufficient to determine the affinities of any arthropod, as Roger has pointed out (1946, p. 59), and hence it seems better to group such isolated carapaces together as follows.

TRILOBITOIDEA or CRUSTACEA *incertae sedis*

Proboscicaris gen. nov.

Type species. Proboscicaris agnosta sp. nov.

Diagnosis. Carapace valves only known, large, with antero-dorsal region produced into a spatulate beak.

Proboscicaris agnosta sp. nov.

Plate 1, figures 1, 2; Text-figure 1

Diagnosis. Anterior beak prominent; length of posterior margin 0.43 to 0.82 of greatest depth of carapace; posterior margin indented at or near midpoint.

Description. Valves elongate, ranging from shallow to deep. Since the orientation of the valves is unknown, the straight to slightly concave margin will be treated as dorsal and the produced region as anterior. Postero-dorsal angle rounded and obtuse; posterior margin slightly indented at or near its midpoint. Ventral margin moderately convex in posterior half to three-quarters of carapace length; strongly concave in anterior region and separating off a tongue-shaped anterior beak. This beak has been lost from USNM 139866 (see Text-fig. 1) and it seems likely that the distinct outlines shown by USNM 139869 and 139873 (Text-fig. 1) are only due to the loss of this region. The absence of a recognizable rim or doublure prevents certainty on this point.

The valves were doubtless joined by a membranous hinge along the dorsal border as in *Canadaspis.* Only one specimen shows evidence of two valves preserved, and this is shown on Text-figure 1, USNM 139872. Only the anterior beak of the right valve is preserved and this is displaced anteriorly relative to the almost complete left valve.

A reticulate pattern may be seen in patchy areas on USNM 139867 and 139873. The wrinkles subparallel to the ventral margin of USNM 139866 (Text-fig. 1) are clearly due to flattening of the originally convex test. Specimens USNM 139867, 139870, 139871, 139873, MCZ 5979/2 and MCZ 5979/3 are blotched by the alga *Morania parasitica* Walcott, previously recorded on *Canadaspis* and figured by Walcott (1919, p. 232, pl. 50, fig. 1) on a carapace of *Hurdia victoria* Walcott.

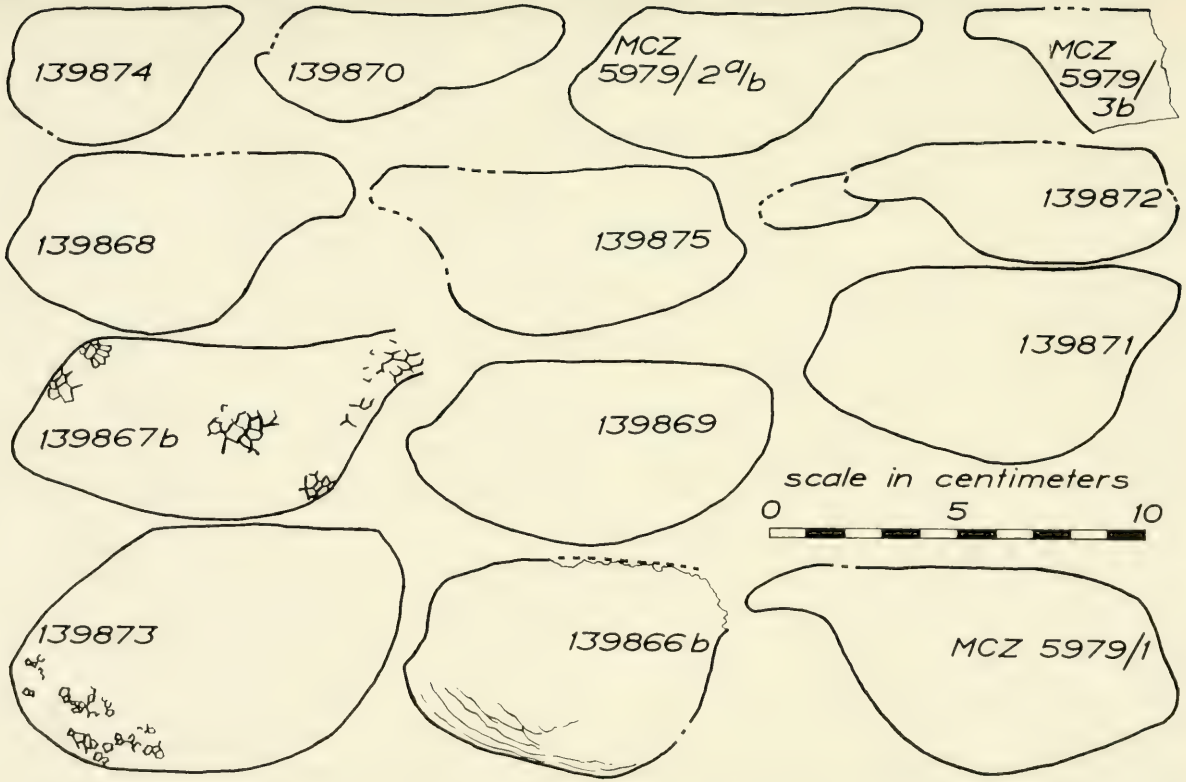

FIG. 1. Outline drawings of thirteen of the fourteen known specimens of *Proboscicaris agnosta* gen. et sp. nov. with catalog numbers indicated. Holotype — USNM 139871.

Remarks. The form of the carapace is so distinct that little confusion is possible with previously described species. Such a small beaked specimen as USNM 139874 approaches *Canadaspis perfecta* (Walcott) in outline, but the posterior and antero-ventral embayments readily distinguish the new form. Some specimens of *Hurdia victoria* in the Museum of Comparative Zoology show an indentation of the ?posterior margin similar to that in *Proboscicaris*, and in addition show an identical reticulation of the carapace surface, so that fragments of the posterior ends of the two forms might prove difficult to distinguish. Large-mesh reticulation also occurs in *Tuzoia* and *Carnarvonia* (Walcott, 1912, pp. 157-158, 165, 187, 189) so that this character is of little value for suggesting relationships. Small-mesh reticulation is visible in species of *Caryocaris*, *Dictyocaris* and *Concavicaris* (as well as in the olenellid trilobites: Raw, 1936; Moore, 1958, fig. 5.22), and in *Ceratiocaris* and *Montecaris* such reticulation can be shown to arise from differential corrosion of the cuticular prisms (Rolfe, 1962a, pp. 45-47). The cuticle of the Burgess Shale specimens is too poorly preserved to ascertain whether this reticulation is sculptural or structural.

Holotype. USNM 139871. Plate 1, figure 2 and Text-figure 1.

Other material. The twelve specimens shown on Text-figure 1: USNM 139866a/b, 139867a/b, 139868-139870, 139872-139875, MCZ 5979/1, 5979/2a/b, 5979/3a/b. Another specimen, USNM 139876, is a fragment of the anterior end only.

Dimensions of holotype. Maximum length parallel to hinge line: 98 mm. Maximum depth perpendicular to hinge line: 52 mm.

Proboscicaris ingens sp. nov.

Plate 1, figure 3; Text-figure 2

Diagnosis. Carapace valves only known; anterior beak relatively small; length of posterior margin *ca.* 0.28 of greatest depth of carapace; posterior margin sigmoidal.

Description. The ventral margin is more of a simple skewed curve than the convex and concave outline of *P. agnosta.* The posterior margin is shorter and hence is situated more dorsally than in *P. agnosta* and in addition this margin is sigmoidal rather than indented. The carapace margin is curled under, except along the dorsal border, suggesting the marginal rim common in the later phyllocarids.

The surface of the carapace is smooth but little is preserved of the original test save blotches of filmy black material. Occasional circular areas of silver sheen on the holotype may represent *Morania parasitica*.

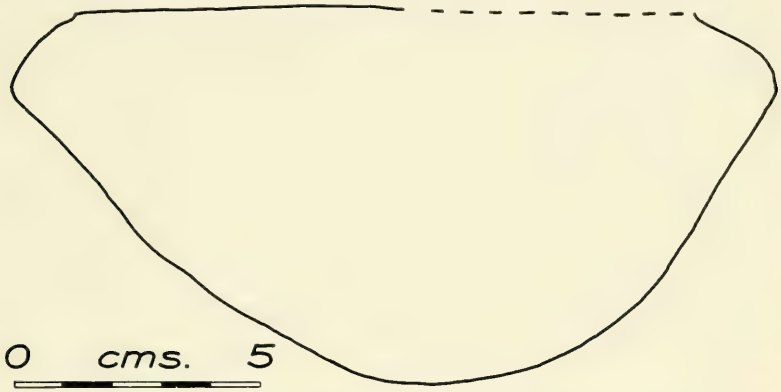

FIG. 2. Outline drawing of the holotype of *Proboscicaris ingens* sp. nov. — USNM 139865b. Postulated anterior to left.

Remarks. Again the carapace shape is distinctive, though the asymmetrical outline recalls that of *Isoxys*, which, however, is smaller and has the anterior and posterior dorsal extremities acuminate rather than truncate.

This species is the largest of the known Burgess Shale arthropods in terms of surface area of the carapace and was doubtless the one which Walcott had in mind when he wrote, "there are also fragments of the carapace of a very large form that possibly may be related to *Hurdia victoria*" (1912, p. 183). Individuals of *H. victoria* may be longer but they are also slenderer. Such large carapaces are of particular interest in this fauna since it is among them that a suitable adult for the hypothetically larval *Waptia fieldensis* might be sought (Fedotov, 1925, pp. 386, 389; Heldt, 1954, p. 180; Tiegs and Manton, 1958, pp. 292, 314; *cf.* Henriksen, 1928, p. 14; Størmer, 1944, p. 100). In this connection is seems worth recalling the striking resemblance of *Marria*, from this same deposit, to a crustacean nauplius (Ruedemann, 1931, p. 8) or metanauplius. A comparable Upper Ordovician form, *Paramarria*, occurs in association with an archaeostracan carapace, *Galenocaris* (Wells, 1944). If *Paramarria* is a naupliar stage, and the larval stage of *Galenocaris*, and its

aspect is not merely due to convergence for a planktonic existence (as that of *Mimetaster* and *Bostrichopus* seems to be), it would contrast with Recent Leptostraca. In the latter group, development is direct, the young hatching at a late stage. Similarly, *Naraoia* might be regarded as a larval merostomoid.

It is possible that *P. ingens* is simply an older instar of *P. agnosta*. However, such radical changes in shape are not common except in early ontogeny, and it seems better to distinguish this form as a separate species.

Holotype. USNM 139865a/b — part and counterpart.

Dimensions of holotype. Maximum length parallel to hinge line: 156 mm. Maximum depth perpendicular to hinge line: 75 mm.

Other material: USNM 139890 — a fragment of the posterior of a carapace valve, which must have exceeded 150 mm. long by 95 mm. deep when complete.

DISCUSSION

The lack of limbs or body segments precludes any discussion of the affinities of this new genus and the problem of classification of these early crustacean-trilobitoid forms has been summarized elsewhere (Rolfe, 1962b).

It seems worthless to classify such isolated carapaces above the generic level in view of the limited number of characters available. Many of the genera attributed to phyllocarid families, or made the types of new families such as the Isoxyidae (junior synonym of Tuzoiidae Raymond, 1935) and Pseudoarctolepididae of Brooks and Caster (1956, p. 13), will need to be brought together under the *incertae sedis* category shown above.

Some idea of the relative abundance of *Proboscicaris agnosta* in the Burgess Shale fauna may be gained from the following list of numbers of individuals of non-trilobite arthropods collected by the 1930 MCZ expedition, and recently curated by the writer:

TRILOBITOIDEA

Burgessia bella Walcott	54
Emeraldella or *?Molaria* spp. indet.	3
Leanchoilia superlata Walc.	12
Marrella splendens Walc.	202
Naraoia compacta Walc.	3

Opabinia regalis Walc.	1
Sidneyia inexpectans Walc.	9
?Yohoia plena Walc.	1

TRILOBITOIDEA or CRUSTACEA *incertae sedis*

Anomalocaris canadensis Whiteaves	*ca.* 22
Canadaspis obliqua (Walc.)	7
C. ovalis (Walc.)	1
C. perfecta (Walc.)	76
C. sp. indet.	12
Fieldia lanceolata Walc.	1
Hurdia triangulata Walc.	1
H. victoria Walc.	16
Isoxys acutangulus Walc.	10
Proboscicaris agnosta sp. nov.	3
Protocaris cf. *pretiosa* Resser	1
Tuzoia retifera Walc.	1
T. sp. indet.	2

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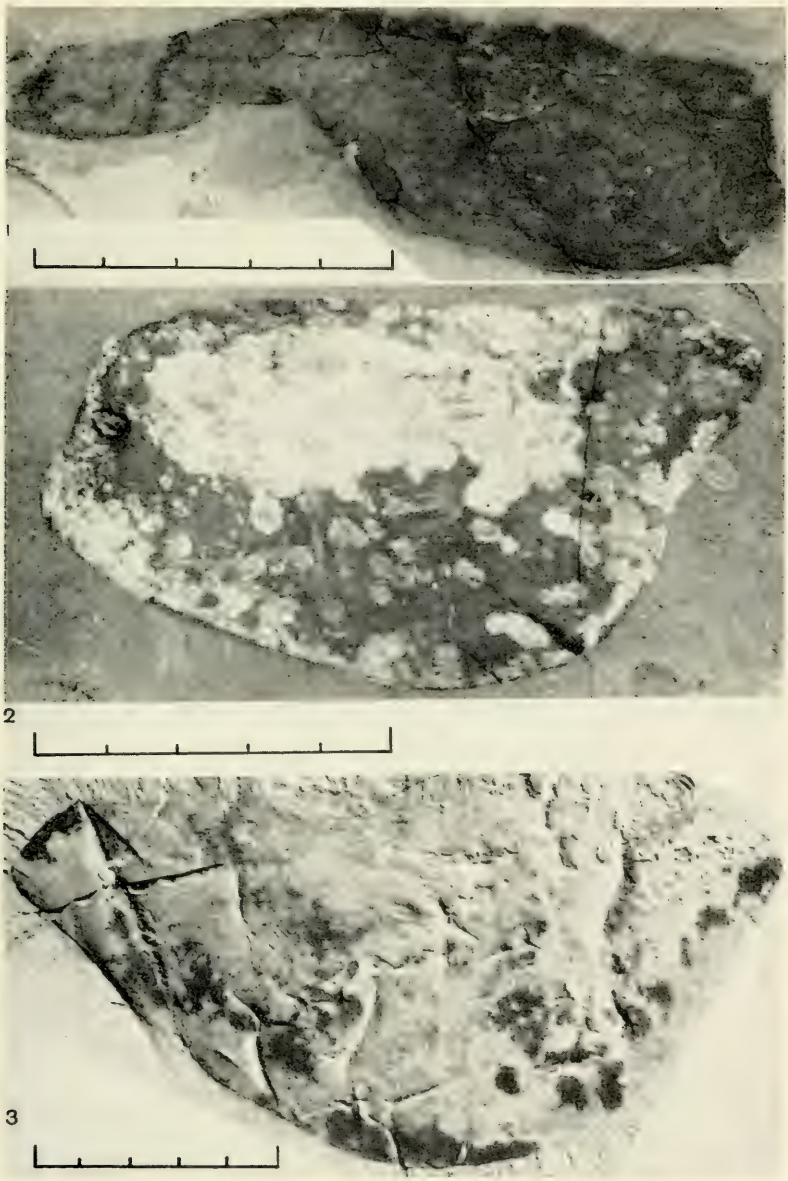

Plate 1

The scale beneath the Figures represents five centimeters.

Figs. 1-2. *Proboscicaris agnosta* gen. et sp. nov. 1. Left valve and displaced anterior beak of right valve of carapace. USNM 139872. 2. Holotype — USNM 139871 with anterior of valve at right. The silver blotches are the encrusting alga *Morania parasitica* Walcott. 3. *Proboscicaris ingens* sp. nov., holotype — USNM 139865b. Postulated anterior to left. From an

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A COMPARATIVE STUDY OF THE RESPIRATORY MUSCLES IN CHELONIA

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INTRODUCTION

The unique skeletal modifications in Chelonia have greatly influenced the morphological features of the soft parts in these animals. Of these modifications the rigid shell formation is the most prominent characteristic feature of the Chelonia; this has made their body wall immovable and hence the normal respiratory movements characteristic of amniotes are lost. This loss of active body wall movements has given much reason for discussion about the respiratory mechanism adapted by the chelonians, and from the time of Malpighi and Cuvier many attempts have been made to explain the phenomenon. Some have suggested that the throat movements similar to those seen in frogs are responsible for bringing about the expirations and inspirations in Chelonia; others have supposed that the movements of the limbs and the neck indirectly effect the expiration and inspiration. Recently McCutcheon (1943) has summarized the evidence that, on the contrary, the movements of certain abdominal muscles, the *diaphragmaticus*,[1] the *transversus abdominis*, the *serratus magnus* and the *obliquus abdominis*, bring

1 A matter of terminology must be mentioned here. McCutcheon (1943) described the flank cavity muscles in *Malaclemys centrata* where the *diaphragmaticus* muscle as described by him seems to be the same as the *muscularis striatum pulmonale* and quite different from the *diaphragmaticus* as described in this paper. Owen (1866), describing the musculature of *Emys europea*, describes the *diaphragmaticus* as formed of three parts originating from the carapace; two parts insert on the wall of the lung while the third one inserts on the plastron. This description compares well with the account given here, except that the two parts of the muscle described by Owen as inserting on the lung are here regarded as the *muscularis striatum pulmonale*, and only the third part which inserts on the plastron is the true *diaphragmaticus*.

about expiration and inspiration. He interprets the throat movements in Chelonia as functioning in olfaction and not in respiration. George and Shah (1954) have studied the respiratory mechanism in *Lissemys* and have confirmed McCutcheon's view that the abdominal muscles are effective for respiratory movements and that the throat movements are only for olfaction. In addition, they have also described the presence of an extra pair of muscles which cover the lungs completely in *Lissemys*. These muscles are composed of striated muscle fibres. On contraction of these muscles the pulmonary air is pushed out of the lungs, and on their relaxation the atmospheric air is taken in. Thus these lung muscles, the *muscularis striatum pulmonale*, aid the action of the abdominal muscles in bringing about the expiration and inspiration.

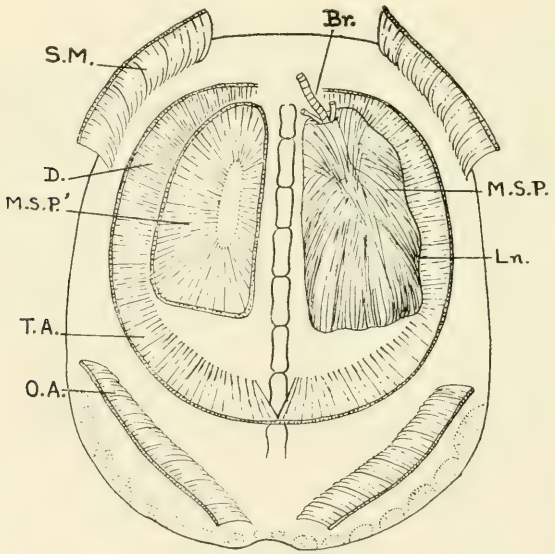

Fig. 1. Diagrammatic sketch of the disposition of the respiratory muscles in Cyclanorbinae where the lungs are completely covered by the *muscularis striatum pulmonale*.

George and Shah (1955, 1958 and 1959) made a comparative study of the abdominal muscles and of the lung muscles in some additional chelonians: *Lissemys punctata* (all three

subspecies), *Geoemyda trijuga*, *Trionyx gangeticus*, *Testudo elegans*, *Malacochersus torneri* and *Eretmochelys imbricata*. According to their observations the lung muscle, the *muscularis striatum pulmonale*, covers the lungs completely in *Lissemys punctata*, partially in *Geoemyda*, while the muscle is totally absent in the rest of the forms they studied. Of the flank cavity muscles the *diaphragmaticus* and the *transversus abdominis* are

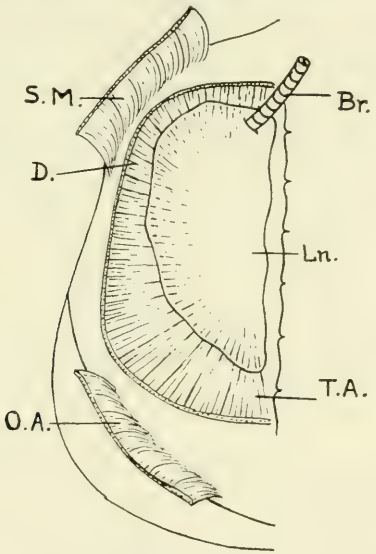

Fig. 2. Diagrammatic sketch of the disposition of the respiratory muscles in Trionychinae.

well developed in *Lissemys* and *Trionyx* where they join with each other to form a continuous muscle sheath covering the visceral organs including lungs. The *diaphragmaticus* in *Geoemyda trijuga* and *Eretmochelys imbricata* does not join with the *transversus abdominis* to form a continuous muscle sheath, but there is a bridge of connective tissue between them. In *Testudo elegans* and *Malacochersus torneri* the *diaphragmaticus* muscle is totally absent leaving only a thin membranous sheath of connective tissue in its place. The other flank cavity muscles, viz. the *serratus magnus* and the *obliquus abdominis* are present with slight variation in all the animals they studied.

In the light of these observations on the respiratory muscles in a very few chelonians, it was thought desirable to examine

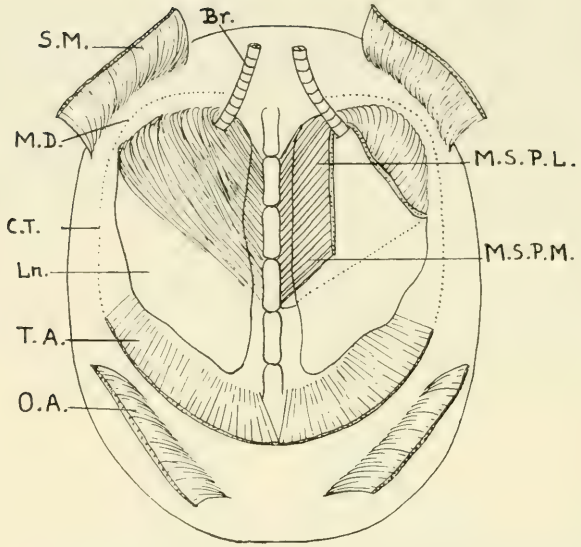

Fig. 3. Diagrammatic sketch of the disposition of the respiratory muscles in *Malaclemys terrapin terrapin*.

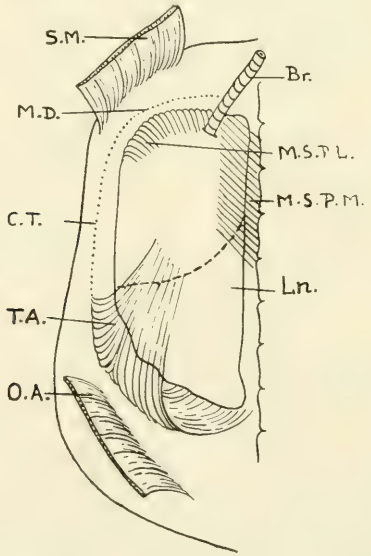

Fig. 4. Diagrammatic sketch of the disposition of the respiratory muscles in *Pseudemys floridana* and *Pseudemys texana*.

more forms representing, as far as possible, almost all the major groups of the order Chelonia, and make a comprehensive comparative study of these muscles to get an overall idea of the morphological features of the respiratory mechanism adapted by the animals of this order.

For this study some fifty different cryptodiran and nine pleurodiran forms were selected. A list of the animals chosen is given below.

This work was carried out at the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts, U.S.A. I am thankful to Dr. A. S. Romer, then Director of the Museum, and Dr. E. E. Williams, Curator of Herpetology, for all the facilities given and for their constant help and encouragement during the course of the study.

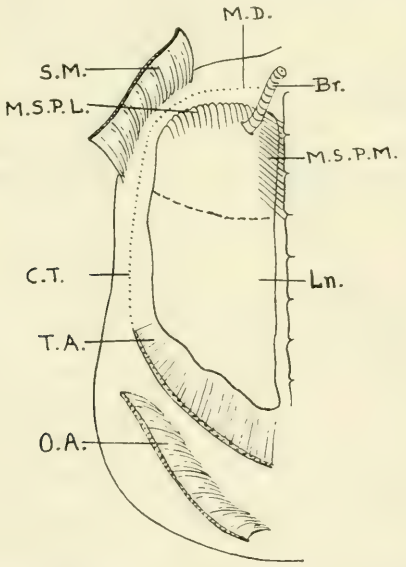

Fig. 5. Diagrammatic sketch of the disposition of the respiratory muscles in Emydinae forms in which the *diaphragmaticus* muscle is absent.

MATERIAL STUDIED

All the animals selected for the study were alcohol preserved and were found in excellent state of preservation. Careful dissections of the flank cavity muscles, the *diaphragmaticus*, the *transversus abdominis*, the *serratus magnus* and the *obliquus*

abdominis and the lung muscle, the *muscularis striatum pulmonale*, were done on these animals and following is the report of the comparative study.

List of chelonians selected for the present study:

CRYPTODIRA

TESTUDINOIDEA

TESTUDINIDAE

Emydinae

Chinemys reevesii
Chrysemys picta dorsalis
Chrysemys picta marginata
Chrysemys picta picta
Clemmys caspica caspica
Clemmys caspica leprosa
Clemmys guttata
Clemmys mutica
Cuora amboinensis
Deirochelys reticularia
Emydoidea blandingii
Emys orbicularis
Geoemyda manni
Geoemyda punctularia funerea
Geoemyda spinosa
Geoemyda trijuga
Graptemys kohni
Graptemys pseudogeographica
Kachuga tectum tectum
Malaclemys terrapin terrapin
Malayemys subtrijuga
Ocadia sinensis
Pseudemys floridana
Pseudemys texana
Terrapene yucatana

Testudininae

Geochelone pardalis
Pyxis arachnoides
Testudo graeca
Testudo hermanni
Testudo horsfieldii
Testudo kleinmanni

CHELYDRIDAE

Kinosterninae

Sternotherus carinatus minor
Sternotherus odoratus

Chelydrinae

Chelydra serpentina

TRIONYCHOIDEA

TRIONYCHIDAE

Cyclanorbinae

Cyclanorbis sp.
Cycloderma frenatum
Lissemys punctata
(all three subspecies)

Trionychinae

Dogania subplana
Trionyx gangeticus
Trionyx sinensis
Trionyx triunguis

CHELONOIDEA

CHELONIDAE

Caretta caretta
Chelonia mydas
Eretmochelys imbricata
Lepidochelys olivacea

DERMOCHELYOIDEA

DERMOCHELYIDAE

Dermochelys coriacea

PLEURODIRA

PELOMEDUSIDAE

Pelomedusa subrufa subrufa
Pelusios subniger
Podocnemis expansa
Podocnemis lewyana
Podocnemis unifilis

CHELIDAE

Chelodina longicollis
Emydura krefti
Hydromedusa maximiliani
Phrynops geoffroana
Platemys platycephala

DESCRIPTION OF THE MUSCLES

Of all the respiratory muscles mentioned above, the lung muscle, the *muscularis striatum pulmonale*, shows the most extreme variation in Chelonia. It is so well developed in the forms belonging to the subfamily Cyclanorbinae that it covers the lung completely while in the other subfamily, Trionychinae, the muscle is totally absent. In *Cyclanorbis* sp. and *Cycloderma frenatum* (Fig. 1) the muscle arises from the carapace in the vicinity of the second and third thoracic vertebrae and also from the lateral side of these vertebrae. The fibres arising from the carapace run over the entire dorsal surface of the lung and when they

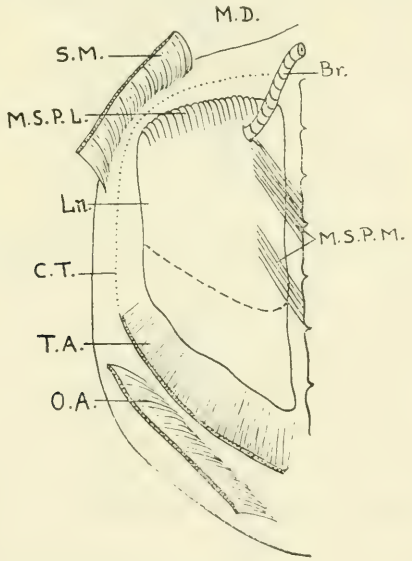

Fig. 6. Diagrammatic sketch of the disposition of the respiratory muscles in *Kachuga tectum*.

reach the outer, anterior, and the posterior limits of the lung they turn onto the ventral side and continue to run towards the entrance of the bronchus. The fibres arising from the lateral side of the thoracic vertebrae run over the medial side of the lung and then come onto the ventral side and reach the entrance of the bronchus. All the fibres of the muscle closely adhere to the wall of the lung. From the place of the origin of the fibres, the muscle could be arbitrarily divided into two parts, a lateral

part which arises from the carapace and a medial part which arises from the lateral side of the thoracic vertebrae. The *muscularis striatum pulmonale* in *Lissemys punctata* (Fig. 1) (George and Shah, 1954) differs slightly from the one in *Cyclanorbis* and *Cycloderma;* the muscle is otherwise very similar in its course and insertion in all the three genera of Cyclanorbinae. In *Lissemys* the muscle arises entirely from the carapace and does not have its lateral part arising from the side of the vertebrae. The muscle in all the forms of the group Cyclanorbinae is

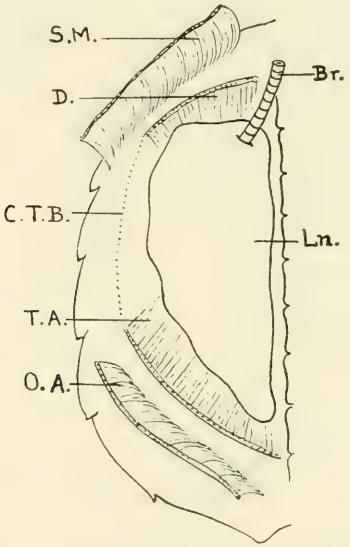

Fig. 7. Diagrammatic sketch of the disposition of the respiratory muscles in marine turtles.

innervated by the branches of the intercostal nerves. As said before, the muscle on its contraction pushes out the pulmonary air of the lungs, and on its relaxation the atmospheric air rushes in.

In *Trionyx gangeticus, Trionyx sinensis, Trionyx triunguis* and *Dogania subplana* (Fig. 2) belonging to Trionychinae, the *muscularis striatum pulmonale* muscles is totally absent.

All the forms belonging to the Emydinae have a *muscularis striatum pulmonale* which partly covers the lung. In this group the muscle shows great variation in different species.

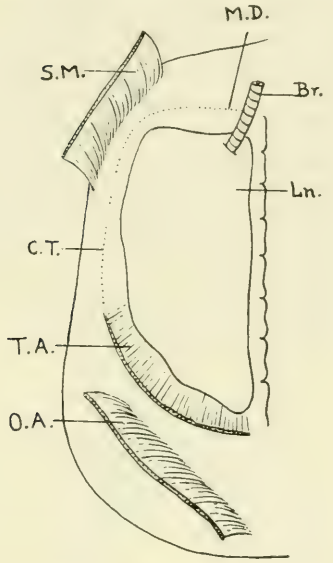

Fig. 8. Diagrammatic sketch of the disposition of the respiratory muscles in Testudininae, except *Pyxis arachnoides*.

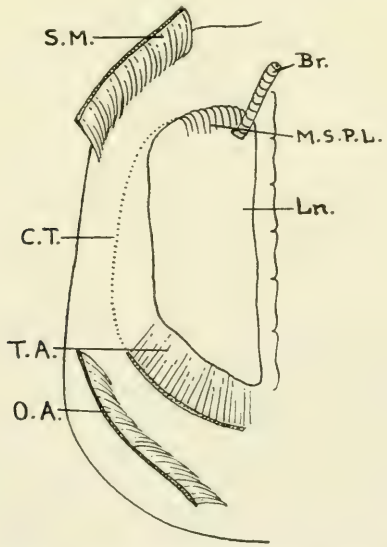

Fig. 9. Diagrammatic sketch of the disposition of the respiratory muscles in *Pyxis arachnoides*.

In *Malaclemys terrapin terrapin, Clemmys caspica caspica, Clemmys guttata, Graptemys pseudogeographica, Graptemys kohni, Cuora amboinensis, Pseudemys floridana* and *Pseudemys texana*, the *muscularis striatum pulmonale*, though only partly covering the lung, is well developed compared to other Emydinae. In these emydines the medial part of the muscle arising from the side of the thoracic vertebrae is well developed and quite extensive, while the lateral part of the muscle with its origin from the carapace, though well developed, is comparatively small

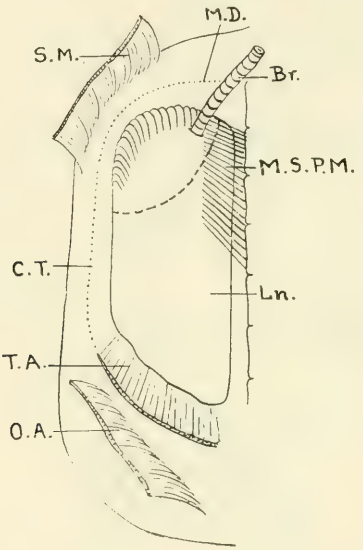

Fig. 10. Diagrammatic sketch of the disposition of the respiratory muscles in Pleurodira forms in which the *muscularis striatum pulmonale* is partial and the *diaphragmaticus* muscle is absent.

in extent. However, in *Malaclemys terrapin terrapin, Graptemys pseudogeographica* and *Graptemys kohni* the lateral part of the muscle is comparatively more developed than in the other emydines listed above. The place of origin of the lateral part of the muscle in these three forms is parallel to that of the medial part of the muscle (Fig. 3). In *Pseudemys floridana* and *Pseudemys texana* the place of origin of the lateral part of the muscle is perpendicular to that of the medial part of the muscle (Fig. 4).

In *Emys orbicularis, Kachuga tectum tectum, Ocadia sinensis, Chrysemys picta picta, Chrysemys picta dorsalis, Chrysemys picta marginata, Deirochelys reticularia, Emydoidea blandingii, Clemmys mutica, Chinemys reevesii, Malaycmys subtrijuga, Geoemyda punctularia funerea* (Figs. 5 and 6), *Geoemyda manni, Geoemyda spinosa,* and *Geoemyda trijuga* (Fig. 12) the medial part of the *muscularis striatum pulmonale* is very poorly developed and only covers a very small portion of the anterior medial side of the lung. The lateral part of the muscle is also less developed compared to that of *Malaclemys* and others and shows variations in its extent, never covering more than a small portion of the anterior and anterolateral side of the lung.

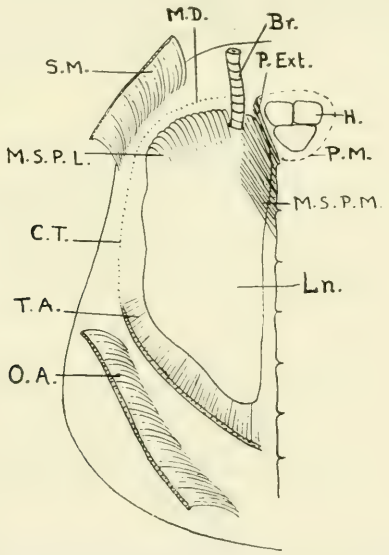

Fig. 11. Diagrammatic sketch of the disposition of the respiratory muscles in *Podocnemis.*

Six species belonging to the Testudininae, *Testudo hermanni, Testudo graeca, Geochelone pardalis, Testudo horsfieldii, Testudo kleinmanni* (Fig. 8) and *Pyxis arachnoides* (Fig. 9) have been examined. In all these except *Pyxis arachnoides* the *muscularis striatum pulmonale* is totally absent and a thin sheet of connective tissue is present in its place. In *Pyxis arachnoides* (Fig. 9) there is a poorly developed lateral part of the *muscularis striatum pulmonale* present, covering only a very small part of the anterior region of the lung. The presence of part of the

muscle in *Pyxis* appears to be a case of an intermediate stage between the typical condition of the Testudininae, on one hand, where the muscle is absent, and that of Emydinae, on the other, in which it is better developed.

In *Sternotherus odoratus* and *Sternotherus carinatus minor,* belonging to Kinosterninae, the *muscularis striatum pulmonale* is similar in its origin, course and insertion to that described for the *Malaclemys terrapin terrapin* (Fig. 3). In *Chelydra serpentina* of the Chelydrinae the muscle is completely absent and instead a thin layer of connective tissue is present in its place.

In *Chelonia mydas, Caretta caretta, Lepidochelys olivacea* and *Eretmochelys imbricata* (Fig. 7), which all belong to the family Chelonidae, the *muscularis striatum pulmonale* is totally absent. Even in *Dermochelys coriacea* (Fig. 7), of the Dermochelyoidea,

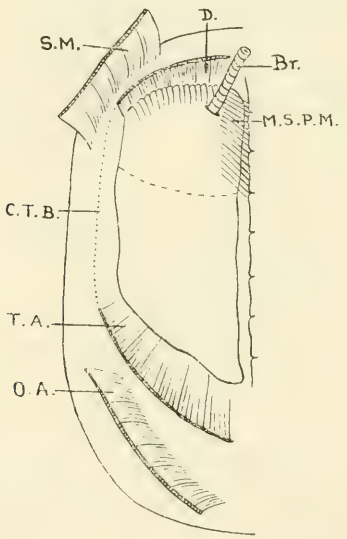

Fig. 12. Diagrammatic sketch of the disposition of the respiratory muscles in such Emydinae as *Geoemyda spinosa,* etc.

the muscle is absent. Thus, it appears that none of the marine forms possess any lung muscle, and that unlike the land forms or the fresh water ones there is no variation in this regard.

All the members belonging to the suborder Pleurodira possess a partial *muscularis striatum pulmonale* rather similar to that seen in the Emydinae (Fig. 5). The members of the genus

Podocnemis show an unusual extension of the *muscularis striatum pulmonale*. In *Podocnemis unifilis* and the other two species of *Podocnemis*, the medial part of the muscle, after its usual origin, runs forward adhering to the medial wall of the lung and (unlike the normal condition where the fibres terminate on the lung near the entrance of the bronchus) after reaching the anterior limit of the lung continues forward and closely adheres to the dorsolateral side of the pericardial membrane. Finally, these fibres insert on the membrane at the level of the anterior side of the auricles (Shah, in press). Such a pericardial extension of the *muscularis striatum pulmonale* is not found in any of the other pleurodirans that were studied. No trace of such an extension is present in any of the Cryptodira, nor does there appear to be any previous record of the presence of a striated muscle layer on the pericardium in any vertebrate.

FLANK CAVITY MUSCLES

The *diaphragmaticus* and the *transversus abdominis* form the expiratory set of the flank cavity muscles in Chelonia, while the *serratus magnus* and the *obliquus abdominis* form the inspiratory set (McCutcheon, 1943; George and Shah, 1954, 1958 and 1959).

In all Chelonia the *transversus abdominis* muscle is well developed. In the Cryptodira studied, the *transversus abdominis* muscle is the most highly developed in the Trionychoidea, and in this group it joins with the anteriorly placed *diaphragmaticus* muscle of the same side to form a continuous muscular sheath which envelops the visceral organs including the lungs. The muscle arises in all the chelonians from the posterior half of the carapace, but the place of origin is not constant in all forms since great variations in its extent are seen in different individuals. In *Pseudemys floridana* and *Pseudemys texana* the *transversus abdominis* muscle extends almost up to the level of the apex of the heart on the ventral side (Fig. 4). In no Emydinae, whether the *diaphragmaticus* muscle is present or not, does the *transversus abdominis* muscle have the extensive spread seen in all the Trionychoidea. In those Emydinae where the *diaphragmaticus* muscle is present, there is a bridge of connective tissue between it and the *transversus abdominis* of the same side. Such a bridge of connective tissue between the *diaphragmaticus* and the *transversus abdominis* muscle is present in all the species of the genus *Geoemyda* and all the marine chelonians.

The *diaphragmaticus* muscle, in all the chelonians in which it is present, arises from the undersurface of the second or third costal plates of the carapace. Its place of origin is oriented transversely with respect to the vertebral column. In all the forms of Trionychoidea (Figs. 1 and 2) the muscle is very highly developed and, as mentioned above, it joins the *transversus abdominis* muscle of its side to form a continuous muscular sheath to envelop the viscera. In some Emydinae the muscle is present (Fig. 12); in others it is absent (Figs. 3, 4, 5, and 6). No members of the Testudinae have the *diaphragmaticus* (Fig. 8); there is a thin layer of connective tissue in its place.

In all the chelonian studies the inspiratory muscles, the *serratus magnus* and the *obliquus abdominis* (Figs. 1 to 11), are present with such slight variation that these are not worth detailed discussion. On contraction of these muscles the volume of the body cavity is increased and thus a negative pressure is created in this cavity and so the lungs expand. On expansion of the lungs the atmospheric air rushes in and in this way inspiration is brought about.

DISCUSSION

From the present study of the respiratory muscles in Chelonia it is evident that there is a great deal of noticeable variation in two muscles, the *diaphragmaticus* and the *muscularis striatum pulmonale*. The variations in these two muscles range from a highly developed condition to a total absence, with all intermediate stages. The other respiratory muscles are always present, and although slight variations in different forms are seen, these are very minor ones.

The presence of the *muscularis striatum pulmonale* in all the Cyclanorbinae, where the muscle covers the lung completely, is regarded as a primitive character which is retained in these forms. The early ancestral chelonians presumably developed these muscles as a substitute for the intercostal muscles lost when their body wall was covered by the rigid shell and could not have the normal movements which are the main component of the respiratory mechanism in all other amniotes. The *muscularis striatum pulmonale* must thus have been of survival value to the early ancestral chelonians, and it is retained fully in all the Cyclanorbinae but shows a gradual trend toward total disappearance in other chelonians. Some chelonians, the Trionychinae, Testudinae and all the marine forms, have totally lost

this muscle. It is quite obvious that the presence of the muscle covering the lung is a hindrance to full expansion of the lungs; it must therefore have developed as a stop gap arrangement to tide over the loss of the body wall movements until some better physiological adaptation for respiration was achieved. Unpublished work by the author on the blood of some chelonians shows some interesting results. The oxiphoric capacity of the blood of *Lissemys punctata* where the *muscularis striatum pulmonale* covers the lungs completely is much less than that of the blood of *Trionyx* or *Testudo elegans* where the muscle is totally absent. The oxiphoric capacity of the blood of *Geoemyda trijuga*, where the *muscularis striatum pulmonale* muscle is incompletely developed (Fig. 12), shows intermediate values. Thus from the study of blood some light is thrown on the new physiological adaptations which have taken place, substituting for some of the morphological adaptations of the primitive forms. More work on the physiology of respiration in different chelonians will be necessary for a better understanding of the problem of respiratory mechanism in this order. Some aspects of this are being worked on at present in my laboratory at the University of Baroda.

ABBREVIATIONS USED IN FIGURES

Br.	Bronchus
C.T.	Connective tissue
C.T.B.	Bridge of connective tissues between *diaphragmaticus* and the *transversus abdominis* muscles.
D.	*Diaphragmaticus* muscle
H.	Heart
Lu.	Lung
M.D.	Connective tissue in place of the *diaphragmaticus* muscle.
M.S.P.	*Muscularis striatum pulmonale* muscle covering the left lung
M.S.P.[1]	*Muscularis striatum pulmonale* muscle cut horizontally and the right lung removed so as to show the place of origin of the muscle
M.S.P.L.	Lateral part of the *muscularis striatum pulmonale*
M.S.P.M.	Medial part of the *muscularis striatum pulmonale*
O.A.	*Obliquus abdominis* muscle
P.M.	Pericardial membrane
P. Ext.	Pericardial extension of *muscularis striatum pulmonale.*
S.M.	*Serratus magnus* muscle
T.A.	*Transversus abdominis* muscle

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BREVIORA

Museum of Comparative Zoology

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AUSTRALIAN CARABID BEETLES X. *BEMBIDION*

BY P. J. DARLINGTON, JR.

Museum of Comparative Zoology, Cambridge, Mass.

This is the tenth in a series of papers on Australian Carabidae. Some earlier parts, including a list of localities at which I collected in 1956-1958 and a discussion of transition of wet forest carabid faunas from New Guinea to Tasmania, are given under References.

The present paper deals with the Australian species of *Bembidion* (*sensu lato*). This is a zoogeographically important genus, which tends to be bi-zonal in distribution, occurring mainly in the north and south temperate zones of the world (Darlington 1959, pp. 332-333). The distribution, ecology, relationships, and possible history of the Australian forms are therefore noteworthy and will be summarized after discussion of the separate species.

I am indebted to Prof. Carl H. Lindroth for dissecting males of all the Australian species and telling me how he thinks they are related to European and North American forms. I could have made the dissections myself, but I am not familiar with the genitalic characters of northern *Bembidion* and could not have interpreted the characters of the Australian species. However, neither Prof. Lindroth nor I have investigated most of the Asiatic species or those of New Zealand or southern South America. This paper is therefore only a limited contribution to the zoogeography of *Bembidion*.

At the time of Sloane's last study of Australian Bembidiini (1921), he knew five Australian species of *Bembidion* and two of *Cillenus*. Two supposed "*Bembidion*" of Blackburn's that Sloane did not know (*hobarti* and *wattsense*) are in fact not *Bembidion* but *Tachys*. I plan to treat them in my next paper. I have series of all five real *Bembidion* known to Sloane and

have seen no other native species, and it may be that these five species of the genus (excluding *Cillenus*) are all that are native in Australia, although it is too soon to be sure about this. References and synonymy of the species are given by Sloane (*op. cit.*) and will usually not be repeated here. The species should be identifiable by the following key, which is based partly on Sloane's key (1921, p. 193). All the species are winged and presumably able to fly, except that the wings are dimorphic in *proprium* (*q.v.*).

Key to Australian Species of Bembidion

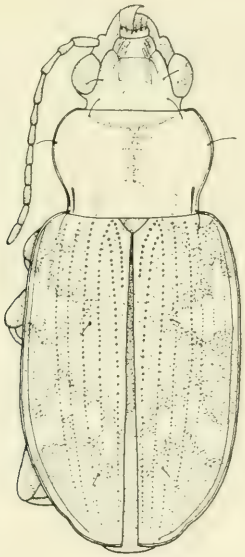
1. Large (*c.* 5.2-6.5 mm.); dull bronze, elytra with 2 incomplete transverse pale fasciae; clypeus with several fine converging grooves on each side (introduced from South America) ..... *brullei*
— Smaller; not marked as above; (native) 2
2. Frontal sulci long, impressed and converging on clypeus; upper surface of insect dull or shining; elytron with 6 or 7 dorsal striae 3
— Frontal sulci shallow and rather short, not crossing clypeus; upper surface dull; elytron with 7 dorsal striae 5
3. Dull brown with vague paler elytral markings; whole upper surface microreticulate; elytron with 6 dorsal striae (stria 7 absent or faint); length *c.* 4.2-4.8 mm. ..... *errans*
— Shining, upper surface not microreticulate; elytron 7-striate; size smaller 4
4. Elytron with 2 seta-bearing punctures on 3rd interval, none on 5th; color black, elytral apices and sometimes lateral subapical spots slightly paler; length *c.* 3.3-3.9 mm. ..... *blackburni*
— Elytral intervals 3 and 5 each with several inconspicuous seta-bearing punctures; color irregular dark brown; length *c.* 2.9-3.4 mm. *proprium*
5. Prothorax transverse, sides not sinuate posteriorly; color much like following species except apical testaceous area of each elytron broken into subapical and apical marks which are often narrowly connected along outer elytral margin and sometimes connected near suture too; length *c.* 3.0-4.0 mm. ..... *jacksoniense*
— Prothorax cordate, sides sinuate posteriorly; color greenish or bronzed with elytral apices conspicuously testaceous, the testaceous areas broadly lunate; length *c.* 4.0-4.7 mm. ..... *opulentum*

Bembidion (Notaphus) brullei (Gemminger and Harold)

variegatum Brullé 1843, p. 44 (not Say).
Bembicidium brullei Gemminger and Harold 1868, p. 409.

Form as figured, broader and less convex than usual in Australian species of genus; bronze, appendages irregularly testaceous and fuscous, elytra with complex but variable pale

marks which usually involve epipleuri, parts of elytral bases inside humeri, marginal channels, apices (rather vaguely), an irregular interrupted fascia before middle often including very elongate pale areas on intervals 7 and 8 and isolated spots on 3rd intervals, and an irregular incomplete post-median fascia; sides of abdomen also pale; upper surface dull, with close reticulate microsculpture, isodiametric on head and pronotum, vaguely



Bembidion brullei (Gemminger and Harold), from between Murray Bridge and Meningie, South Australia.

transverse (but nearly isodiametric) on elytra. *Head* .76 and .76 width prothorax (in ♂ ♀ measured); eyes large and prominent; antennae of moderate length, middle segments *c.* 2½X long as wide; front slightly convex; frontal grooves subparallel (slightly curved) and poorly defined on disc, converging and more sharply impressed across clypeus, and latter with additional fine longitudinal (converging) grooves or wrinkles; mentum with entire tooth. *Prothorax* transversely subcordate with rather broad base; width/length 1.45 and 1.44 (in measured ♂ ♀); base/apex 1.19 and 1.17; base/head 1.07 and 1.06; sides broadly arcuate for much of length, moderately sinuate before basal angles; latter well defined and nearly right or slightly

obtuse; lateral margins moderate, each with usual 2 setae; disc convex, with anterior transverse impression poorly defined, middle line distinct but slightly abbreviated at both ends, basal transverse impression poorly defined; baso-lateral impressions deepest inwardly, bottoms irregular or slightly convex, slightly wrinkled but not much punctate, limited externally by longitudinal carinae distinct from prothoracic margins. *Elytra c.* ⅓ wider than prothorax (E/P 1.36 and 1.35); humeri prominent but rounded; sides subparallel for much of length; margins moderate (wider than in *opulentum*), ending anteriorly opposite ends 6th striae (opposite 5th in *opulentum*), forming translucent shelves before subapical sinuations; striation entire, striae slightly impressed and rather strongly punctate especially on disc; intervals slightly convex, 3rd with 2 seta-bearing punctures about ⅓ from base and less than ⅓ from apex. *Inner wings* fully developed. *Lower surface* microreticulate but mostly not distinctly punctate; anterior process of metasternum strongly margined between middle coxae, the margin strongly rounded-angulate at middle. *Legs* without obvious distinctive characters. *Secondary sexual characters:* ♂ with 2 segments each front tarsus moderately dilated and squamulose below; ♂ with 1, ♀ 2 setae each side last ventral segment. Length *c.* 5.2-6.5; width *c.* 2.0-2.6 mm.

Known in Australia only from six specimens taken by myself beside the road between Murray Bridge and Meningie, South Australia, September 1957, probably beside one of the series of more or less saline lakes near the mouth of the Murray River. However, my collecting there was done under difficulty, in the face of light rain driven by strong wind, and I did not distinguish the species in the field. Specimens of *Bembidion errans* and *proprium* were taken on the same occasion.

Superficially, this species looks rather like *Bembidion* (*Notaphus*) *dentellum* Thunberg and related species of the Northern Hemisphere, and Prof. Lindroth says its genitalic characters are those of a true *Notaphus:* "The armature of the internal sac, even in details, comes very close to that of *approximatum* Lec. and *coloradense* Hayw." of North America. The sculpture of the clypeus of *brullei* is distinctive but, I think, not of subgeneric value.

I was on the point of describing this as a new Australian species when I discovered specimens of it in the Museum of

Comparative Zoology from South America, from several localities in northern Argentina. It was described more than a hundred years ago from specimens taken on the seashore at Montevideo, and it is apparently common in the La Plata region and at Córdoba, Argentina. It has presumably been introduced into southern Australia by shipping.

Bembidion (Ananotaphus) errans Blackburn

Netolitzky (1931b, pp. 181-182) made this the type of subgenus *Ananotaphus,* which may be considered to include also the two following species: *proprium* Blackburn and *blackburni* Csiki. The three species in question are somewhat alike in form and agree in having deep frontal sulci, and the male genitalia "show a certain, though not very evident, agreement in the internal sac" (Lindroth). However, the three species differ considerably among themselves, and their relationship to other subgenera is doubtful, so far as the genitalic characters are concerned.

Blackburn and also Sloane (1921) thought that *errans* occurred only near the coast, and I agree, although it is not confined to obviously saline habitats. It has been previously recorded from southern Western Australia, South Australia, and Victoria. I have a series from southern Western Australia, from several localities including the vicinity of Perth and Pemberton, collected by H. Demarz, and I took two specimens between Murray Bridge and Meningie, South Australia, and four near Hobart, Tasmania. In Western Australia Sloane found it "on the muddy margin of the Vasse River within the tidal influence," and some of Demarz's specimens were taken at Mandura salt lake. My South Australian specimens were probably taken by slightly saline ponds near (east of) the mouth of the Murray River (see under preceding species). My Tasmanian specimens were on the grassy-muddy bank of a small pond in flat, lowland country north of Hobart. This was essentially a fresh-water habitat, but it was only a few miles from the coast and there may have been a trace of salt there. A series of *B. proprium* and one specimen of *blackburni* were taken at the same place.

Bembidion (Ananotaphus) proprium Blackburn

Sloane (1921) knew this species too only from localities on or near the coast of southern Australia, including South

Australia, Victoria, and southern New South Wales (Wollongong). One of his specimens was "beside a little rivulet near where it entered the sea" (presumably at Wollongong). My mainland specimens too are from coastal localities, from between Murray Bridge and Meningie (see under *B. brullei*) and between Meningie and Kingston, South Australia (taken by myself), and from Seaford, Victoria (taken "under beach drift" by W. L. Brown). However, I took a series in Tasmania, north of Hobart, beside fresh water, though still near the coast (see under *errans*). The species thus seems to have about the same ecological distribution as *errans*.

My seven mainland specimens are all fully winged. Most of the sixteen from Tasmania have the inner wings somewhat reduced, about as long as the elytra, slightly folded or crumpled at apex, and evidently unfit for flight, but one of the Tasmanian specimens is fully winged or nearly so.

Bembidion (Ananotaphus) blackburni Csiki

Csiki 1928, p. 159.
dubium Blackburn 1888 (not Heer, not Wollaston).

Sloane (1921) records this species from South Australia, Victoria, and southern New South Wales, and notes that it occurs beside fresh water, in some cases much farther from the coast than the preceding species. I took it at Winchelsea, Victoria, and found it common in Tasmania. It occurred in wet places at low altitudes near Hobart (see under *errans*) and near Ellendale, but it was commoner on the mountains, near Lake St. Clair (over 2400 ft. altitude) and Great Lake (*c.* 3400 ft.), for example. On the mountains in Tasmania *blackburni* occurs not only beside standing water and in other wet places but sometimes also on wet, open heaths near and above tree line. Here it runs in sunlight in and on the dense mats of moss and other vegetation that cover much of the ground in open places. This is a true subantarctic habitat. *Bembidion blackburni* is the only Australian species of the genus that reaches a subantarctic habitat.

On the wet mountain heaths, *B. blackburni* is a member of a small association of superficially similar species of small black Carabidae including *Cyphotrechodes gibbipennis* (Blackburn), *Amblystomus nigrinus* Csiki (*niger* Blackburn), and *Euthenarus nigellus* Sloane. These species look so much alike, superficially, that it is not easy to distinguish them in the field with the naked

eye. They occur together on warm days on wet moss pads, etc., on the mountain heaths as well as in other wet places. This is a striking example of convergence of species of unrelated carabid genera. I do not know its ecological significance. I should add that, although these species occur together under some circumstances, they do not have identical ecological limits elsewhere.

Bembidion (Philochthus) jacksoniense Guérin

[Subgenus *Sloanephila* Netolitzky is here declared a synonym of *Philochthus*, for reasons given below (new synonymy).]

See Sloane (1921, p. 193) for synonyms and references, and see Netolitzky (1931b, p. 182) for subgenus *Sloanephila*, based on this species. However, Netolitzky himself notes the great similarity in most characters of *jacksoniense* and species of the northern (Europe, western Asia, North Africa, etc.) subgenus *Philochthus*, and Prof. Lindroth finds "general agreement in the arrangement of the internal sac of the male genitalia in *jacksoniense* and subg. *Philochthus* . . . ," and it seems to me there is more to gain by recognizing the relationship and putting *jacksoniense* in *Philochthus* than by stressing the differences. Netolitzky says the principal difference is that the metasternal process between the middle coxae is margined in the northern *Philochthus*, not in *jacksoniense*. Netolitzky adds that in this character and in frontal sculpture *jacksoniense* closely resembles *B. "Notaphomimus"* (=*Notaphocampa*) *opulentum* (below). I think these facts may indicate (1) a close relationship between *jacksoniense* and the northern *Philochthus* and (2) a less close one between *Philochthus* and *Notaphocampa*, with *opulentum* perhaps in some ways a connecting link.

Sloane says *jacksoniense* is found over the whole continent of Australia, beside fresh water, and this is probably essentially true. However, it may be absent in small areas in the east and perhaps in larger ones in the north (I am not sure about this) and it has not yet been found in Tasmania, and it certainly occurs in brackish and perhaps alkaline habitats (inland) as well as by strictly fresh water. It is very common in Western Australia but less so in the east, although I have specimens from several eastern localities ranging from Townsville in tropical Queensland south to the Blue Mountains of New South Wales and Mt. Kosciusko. In some localities it occurs with the following species, *opulentum*. In light-trap material from Cooper Crossing, Lake Eyre, it is represented by a few specimens among many *opulentum*.

Bembidion (Notaphocampa) opulentum Nietner

[Subgenus *Notaphomimus* Netolitzky is here declared a synonym of *Notaphocampa*, for reasons given below (new synonymy).]

sobrinum auct. (not Boheman).

Sloane (1921, p. 193) gives Australian synonyms and earlier references to this species. Netolitzky (1931b, pp. 175-178) makes an (I think) unnecessary special subgenus, *Notaphomimus*, for it. Except for the difference in frontal sculpture, which I think is over-stressed by Netolitzky, *opulentum* seems very close to *Bembidion* (*Notaphocampa*) *niloticum* Dejean, and the two species are closely allied in genitalic characters (Lindroth).

I have discussed the distribution of *opulentum* ("*sobrinum*") recently (1959, p. 339), but my statement that the species ranges from Africa through tropical Asia, etc., was apparently wrong, although made on good authority (Netolitzky, Andrewes). There seem to be two slightly different species: *foveolatum* Dejean (*sobrinum* Boheman) of Africa, Madagascar, etc., and *opulentum* Nietner of the Oriental-Australian region (see Jeannel 1946, pp. 370-371, and Basilewsky 1952, p. 177). *B. opulentum* occurs through tropical Asia, part (but not all) of the Malay Archipelago, part of tropical and south temporate eastern Australia, and apparently also in New Caledonia. It exhibits some geographical variation (Netolitzky, *loc. cit.*): the Australian form can be called subspecies *riverinae* Sloane. In Australia it is widely distributed in the eastern part of the continent at least from the latitude of Townsville south to Tasmania and west to South Australia, but I do not think it has yet been found in Western Australia. (Sloane knew it only from Queensland, New South Wales, and Victoria.) It usually occurs near the margins of standing or slowly moving fresh water. Six specimens that I took behind the bank of the Burdekin River near Charters Towers, Queensland, in March 1958, were running on wet mud and beside a stagnant pool of flood water. A specimen from near Waratah, Tasmania, was taken on a log floating in water at the side of a small pond. And three from west of Renmark, South Australia, September 1957 were, I think, taken on mud behind the bank of the Murray River. However, the species apparently occurs also in inland saline areas, for I have a long series taken at light at Cooper Crossing, Lake Eyre, South Australia, in February 1956 (collected by Dr. G. F. Gross). That this species is so widely distributed in Asia but has not yet spread through the whole of Australia suggests that it has reached Australia

comparatively recently, possibly by way of the Lesser Sunda Islands and Timor, for it does not seem to occur in New Guinea or Cape York.

Bembidion, subgenus Cillenus

Cillenus is commonly considered a subgenus of *Bembidion*. Its gross range is from Europe and China to Australia, Tasmania, and New Zealand, but it is strictly coastal. Different species of it occur by running water near the coast, or on ocean beaches, or actually between the tide lines. I have discussed its distribution and possible history elsewhere (1953; 1959, pp. 333-334).

Two species of *Cillenus* are known from (eastern) Australia: a larger, duller one (*albovirens* Sloane) from tropical Queensland (from Townsville, *not* Cairns as incorrectly stated by Sloane in 1921), and a smaller, more slender, more shining one (*mastersi* Sloane) from Sydney and the north coast of Tasmania. Both species probably live on the ocean beach. Both are (irregularly) testaceous, as beach-living Carabidae often are. Both Australian species are fully winged and one or both probably fly. My single specimen of *albovirens* probably flew to light at Townsville, although I did not actually see it do so. Some other *Cillenus* in other regions including New Zealand are flightless.

SUMMARY AND DISCUSSION

The five native Australian species of *Bembidion* (excluding *Cillenus,* which has evidently had an independent history) are distributed as follows. The three species of subgenus *Ananotaphus* occur in the southern part of Australia, and all of them extend to Tasmania too. Of these three, *errans* and *proprium* apparently occur only at low altitudes near the coast, sometimes in saline but also sometimes in fresh or nearly fresh habitats beside water, while *blackburni* is more widely distributed. It sometimes occurs at low altitudes with the two other species, but it has also entered the subantarctic zone on Tasmanian mountains. *B.* (*Philochthus*) *jacksoniense* occurs almost throughout Australia (but not Tasmania) in both fresh and saline (interior) habitats, usually beside standing or slowly moving water. And *B.* (*Notaphocampa*) *opulentum* is widely distributed in the Orient and in tropical and south temperate eastern Australia. It reaches Tasmania but apparently not Western Australia. It occurs in about the same variety of habitats as *jacksoniense*.

These five native Australian species of *Bembidion* are apparently descended from three successive invaders. The first was the ancestor of the endemic subgenus *Ananotaphus*, which has differentiated in Australia and formed three very distinct species. All three are now confined to the southern edge of Australia plus Tasmania; one of the three (*blackburni*) extends into subantarctic habitats on mountains in Tasmania; and one (*propriium*) is undergoing wing atrophy. This looks like an early stage in penetration of the southern cold temperate zone by an originally tropical or northern winged group of Carabidae, and evolution of a derivative flightless stock adapted to southern cold temperate habitats. The ancestor(s) of the Australian and Tasmanian "*Trechus*" may have gone through a stage like this.

The second invader was the ancestor of *Bembidion* (*Philochthus*) *jacksoniense*. The latter has spread throughout Australia (but not Tasmania) and is now a thoroughly distinct species, although its relationship to the northern species of the subgenus is still clear. In southern Australia it overlaps the edge of the range of the species of *Ananotaphus* but (in my experience) it does not often actually occur with them and perhaps does not compete with them very much now, although it may limit their distribution northward.

The third invader is *Bembidion* (*Notaphocampa*) *opulentum*. The fact that this species is now widely distributed in southern Asia (with a very close relative in Africa) but has apparently not yet spread through the whole of Australia, and the fact that the Australian population is only subspecifically differentiated, suggest that the species has reached Australia rather recently. In eastern Australia it occurs with *jacksoniense*, in the same habitats. The two species may compete, and *opulentum* may be replacing *jacksoniense*, which seems to be much less common in eastern Australia, where *opulentum* occurs, than in the west, where *opulentum* does not occur.

This history of three successive invasions, the later invaders perhaps competing with and modifying the distributions of earlier ones, accounts very well for the present distribution of *Bembidion* in Australia. The question then is, what has been the history of the ancestral forms outside Australia?

Bembidion is now dominant in the north temperate zone but is very poorly represented in the tropics, where the genus is replaced by swarms of *Tachys*. The obvious, but not necessarily the correct, guess, therefore, is that the three *Bembidion* that have invaded Australia have somehow crossed the tropics from

the north temperate zone. This would be consistent with the distribution of *Philochthus*, which is now wholly north temperate except for *jacksoniense* isolated in Australia.

However, another, perhaps more probable history can be suggested. The endemic Australian subgenus *Ananotaphus* vaguely resembles *Notaphocampa* in form. *Ananotaphus* has deep frontal sulci and *Notaphocampa opulentum* has shallow ones, but *opulentum* is very close to *Notaphocampa niloticum* Dejean in most characters including male genitalia (Lindroth), and *niloticum* has deep frontal sulci. *Ananotaphus* and *Notaphocampa* are in this way linked by *niloticum*, which, incidentally, ranges from North Africa across tropical Asia north to temperate Japan. Similarities between *Notaphocampa opulentum* and *Philochthus jacksoniense* are noted under the latter in the preceding pages, and *jacksoniense* is clearly related to northern species of *Philochthus*. These are hints that *Ananotaphus*, *Notaphocampa*, and *Philochthus*, which include all the *Bembidion* (except *Cillenus*) native in Australia, *may* belong to one group which has had a rather complex evolutionary and geographical history, and the group may have been primarily tropical. *B. opulentum* and *niloticum* are widespread in the tropics now; all the Australian *Bembidion* are salt-tolerant, which is characteristic of tropical *Bembidion* (Darlington 1953, p. 14), and at least one European *Philochthus* (*aeneum* Germar) is salt-tolerant too (Lindroth); and evolution in the tropics would facilitate the successive invasions of Australia that have occurred.

I suggest, then, that subgenera *Ananotaphus*, *Philochthus*, and *Notaphocampa may* all be derived from one salt-tolerant group of *Bembidion* that has evolved primarily in the Old World tropics, has invaded Australia three times, and has invaded the north temperate zone at least twice, once as *Philochthus* in Europe, etc., and once as *Notaphocampa niloticum* in Japan. This hypothetical history cannot be critically tested until the phylogeny of the whole genus *Bembidion* is better understood. Genitalic characters do *not* clearly confirm it. If the forms in question have evolved as suggested, their history has probably been complex and may have involved additional groups of *Bembidion* that have not reached Australia.

Cillenus is another, independent subgenus of *Bembidion* (perhaps it should be considered a related genus) that has crossed or evolved in the tropics, in saline habitats, and reached Australia (Darlington 1953: 1959, p. 333).

It is noteworthy that, although several stocks of *Bembidion* have reached the western part of the Malay Archipelago from Asia apparently by "mountain hopping," by somehow dispersing from mountain to mountain and from island to island at considerable altitudes (Darlington 1959), none has reached Australia or New Guinea in this way. No *Bembidion* has been found on mountains in New Guinea, and the Australian species are primarily lowland forms and seem to be descended from salt-tolerant ancestors that crossed or evolved in the tropics at low altitudes.

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BREVIORA

Museum of Comparative Zoology

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NEW WORM-LIZARDS (*ANCYLOCRANIUM* AND *AMPHISBAENA*) FROM SOUTHEASTERN TANGANYIKA TERRITORY

BY ARTHUR LOVERIDGE

1. ANCYLOCRANIUM

On the 27th May, 1959, Mr. C. J. P. Ionides collected at Newala an *Ancylocranium* which, later that same year, he donated to the British Museum (Nat. Hist.). While expressing the hope that more material would be forthcoming, I tentatively identified it with *A. barkeri* Loveridge (1946, Proc. Biol. Soc. Washington, vol. 59, p. 73, figs.), a species then, as now, known only from the ♂ holotype (M.C.Z. 48950).

Last year Mr. Ionides was successful in securing six additional *Ancylocranium* from Newala, the most southerly record known for any member of this peculiar genus. I find that all six differ from *A. barkeri* of Lindi District in precisely the same characters as did the first, as recorded in my manuscript notes. Consequently, I propose to designate these Newala *Ancylocranium* as a southerly form of *barkeri*, viz.

ANCYLOCRANIUM BARKERI NEWALAE subsp. nov.

Holotype. Museum of Comparative Zoology No. 67001 (Ionides No. 9356), a presumed ♂, from Newala, Southern Province, Tanganyika Territory. Collected by C. J. P. Ionides, Esq., on 12th June, 1961.

Paratypes. Ionides Nos. 8844, 9351-3, 9355, 9359, of which three are now in the Museum of Comparative Zoology (M.C.Z. 67002-4) and three in the British Museum Nat. Hist.) (BM 1959.1.5.18, 1962.177 and 1962.178).

Diagnosis. Head shields substantially the same as figured for *A. barkeri* from which, however, it may be distinguished as follows:

Median ventrals about six times as broad as their fellows: complete caudal annuli five or less.

27 (18 + 9) or 29 (18 + 11) segments in a midbody annulus; 205-215 annuli on body, normally 3 on underside of tail from post-anal ring to conical tip; known only from 7 specimens from Newala ..... *b. newalae*

31 (20 + 11) segments in a midbody annulus; 222 annuli on body, 4 on underside of tail from post-anal ring to conical tip; known only from ♂ holotype ex Mbemkuru River, Lindi district ..... *b. barkeri*

Median ventrals scarcely broader than their fellows; complete caudal annuli nineteen or more.

32 (16 + 16) or 34 (18 + 16) segments in a midbody annulus; 301-327 annuli on body, 19-23 on underside of tail; known from 7 specimens ex Kilwa and also Mtene, Rondo Plateau (Ionides writes me that he has since obtained 20 more from the Rondo Plateau, but these have not been studied) ... *ionidesi*

Description. Rostral enormous, compressed, arched, with sharp cutting edge; remaining head shields also as in the typical form except that the median upper labial is higher and relatively larger: also there is only a single anterior chin-shield (i.e. postmental) in all paratypes though that of the type (which is the youngest) bears a faint trace of a longitudinal groove.

Segments in a midbody annulus 27 (18 + 9) (in two paratypes 29 (18 + 11)); annuli on body 205 (208-215 in paratypes): annuli on underside of tail from post-anal ring to conical tip 3 (4 in I 9353 only), above tail 6 (7 in all paratypes); anals 5 (as a result of the fusion of the median pair seen in *b. barkeri*, shown by traces of a longitudinal suture in *b. newalae* paratypes I 9351-9352).

Color. In alcohol. Rostral horn-colored, rest of head and body white (? flesh-pink in life), tip of tail purplish brown, the pigmentation extending backwards on the upper surface to beyond its conical end, and undoubtedly serving as a pseudo-head for the amphisbaenid while burrowing.

Size. Total length of holotype ♂, 228 (218 + 10) mm., which is the smallest of the series. Largest, apparently a ♀, 255 (245 + 10) mm. is now in the British Museum.

Discussion. Sexing. None of the seven specimens appears to be breeding. As indicated above, *b. newalae* is the most specialized of the three *Ancylocranium* occurring in Tanganyika Territory. Its very short tail renders sexing difficult without damage, but the type of *b. barkeri* was a verified ♂ in which the tail length was included 24.1 times in its total length. Quite probably tail length is no indication of sex in this species, but if it is one might expect ♂ ♂ to have longer tails. If this is the case then four of the Newala lizards are likely to be ♂ ♂ and three (I 9352, 9355, 9359) are ♀ ♀. In that event the largest example, whose measurements are given above, would be a ♂, whereas when I examined it two years ago I thought it a ♀.

In 7 *b. newalae*, ? ♂ ♂ : tail 22.8 to 25.6 times in total length.
? ♀ ♀ : tail 26.1 to 29.3 times in total length.

In 1 *b. barkeri*, ♂ : tail 24.1 times in total length.

In 7 *ionidesi*, ? ♂ ♂ : tail 10.5 to 11.7 times in total length.
♀ : tail 12.7 times in total length.

For figures and description of the strikingly different *ionidesi* see Loveridge, 1955, Journ. East African Nat. Hist. Soc., vol. 22, p. 177, figs.

2. Amphisbaena

The genus *Amphisbaena* furnishes us with an interesting series of stages in the specialization of worm lizards by reduction of head shields, annuli, etc. From the same district in which the *Ancylocranium* was discovered, two more undescribed amphisbaenids have been obtained by Mr. Ionides. Were it not for the fact that his name already figures in both genera as a result of earlier discoveries made by him, one would like to show appreciation for his generosity in enriching the collections of the Museum of Comparative Zoology and British Museum (Nat. Hist.) by naming one of these novelties after him. Instead, and as they may eventually be assigned subspecific rank, it is as well to name each one after its type locality.

Newala, situated on the edge of the Makonde Plateau at 2,600 feet, is headquarters for the district of the same name and some sixty air miles from the Rondo Plateau where occurs another member of the genus with a quite distinctive arrangement of head shields. The new species may be known as:

AMPHISBAENA NEWALAENSIS, sp. nov.

Holotype. Museum of Comparative Zoology No. 67005 (Ionides No. 9117), a ♂ from Newala, Newala District, Southern Province, Tanganyika Territory. Collected by C. J. P. Ionides, on 19 January, 1961.

Paratypes. Ionides Nos. 9112, 9114-6, 9118-22, of which four are now in the Museum of Comparative Zoology (M.C.Z. 67006-9), and five in the British Museum (Nat. Hist.). Collected by Ionides from 17 to 20 January, 1961.

Diagnosis. Referable to the subgenus *Cynisca*, in which it is intermediate between *A. ewerbecki* (Werner) with whose head squamation *newalaensis* agrees, and *A. rondoensis* Loveridge, with which it concurs in the number of segments in a midbody annulus. Trends may most readily be seen from the following key embracing variational range—approximately 20 in each of the other three species, of each of which I have seen 50 or more specimens.

Posterior temporal lacking (being fused with parietal).

20 (10 + 10) segments in a midbody annulus; 227-247 annuli on body, 23-28 on tail: Rondo Plateau . . . . . *rondoensis*

Posterior temporal present immediately below parietal.

20 (10 + 10) segments in a midbody annulus; 239-255 annuli on body, 22-24 on tail: Makonde Plateau . . . . . *newalaensis*

22 (10 + 12) segments in a midbody annulus; 252-277 annuli on body, 22-27 on tail: Nanguruwe, Newala . . . . . *nanguruwensis*

24 (12 + 12), *very* rarely 22 (10 + 12) segments in midbody annulus; 264-280 annuli on body, 25-28 on tail: Mbanja and Lindi, Lindi District . . . . . *ewerbecki*

Description. Due to fusing of the surviving head shields in the subgenus *Cynisca*, their complicated nomenclature is somewhat difficult to follow. The student is therefore referred to figures 22 (*ewerbecki*) and 23 (*rondoensis*) on pages 393-394 of my Revision of the African Lizards of the Family Amphisbaenidae (1941, Bull. Mus. Comp. Zool., vol. 87, no. 5). The lateral view of *ewerbecki* there shown, will be found to correspond with the head of *newalaensis* in displaying behind the temporal a scale (posterior temporal) immediately below the large parietal. This applies to all ten Newala lizards, as it did to all fifty *ewerbecki* that I collected at Mbanja on the Lindi coast. Viewed from above, the parietal suture of both *newalaensis* and *nanguruwensis* is markedly shorter than as figured for

ewerbecki. Also in both new species, immediately behind the parietals there are frequently traces of occipitals resulting from a marked tendency to enlargement of the median pair of scales in the first annulus.

Even so I have included this annulus as the first body annulus and counted backwards to, and including, the one bearing pores in males, i.e. the one immediately preceding the anals.

Segments in a midbody annulus 20 (10 + 10), as is also the case in every paratype; annuli on body 241 (239-255 in paratypes, viz. 239-243 in ♂ ♂, 246-255 in ♀ ♀) of which the median pair of ventrals are *only* about 1½ times as broad as the adjacent ones; annuli on underside of tail *from* post-anal ring to conical tip 24 (as in all paratype ♂ ♂, 22-23 in three ♀ ♀); anals 6 (5 in one paratype, due to fusion), the median pair much enlarged, the immediate flanking pair of laterals transversely divided (or entire in some paratypes).

Color. In alcohol. Grayish white (? flesh-pink in life), uniform except for the *extreme* tip of tail which is purplish.

Size. Total length of holotype ♂, 144 (127 + 17) mm., largest ♂ in the series; largest ♀ (I 9114), 152 (136 + 16) mm.

In the six ♂ ♂ the tail is included in the total length 8.4 to 9.3 times; in the three undamaged ♀ ♀ from 9.5 to 10.4 times.

Amphisbaena nanguruwensis sp. nov.

Holotype. Museum of Comparative Zoology No. 67010 (Ionides No. 9249), a ♂ from Nanguruwe, ca. 1600 feet, 8 miles south of Newala, Newala District, Southern Province, Tanganyika Territory. Collected by C. J. P. Ionides, on 16 May, 1961.

Paratypes. M.C.Z. 67011-19 (Ionides Nos. 9250-9355), being 37 ♂ ♂ (all used for statistics) and 69 ♀ ♀ (of which 62 were measured but only 42 had annuli counted). With same data as type but collected 12-16 May, 1961.

Diagnosis. See *Diagnosis* for *A. newalaensis*, where the preliminary paragraph and key are equally applicable to *nanguruwensis*.

Description. Again, see remarks under *Description* of the preceding species, for the head shields of *nanguruwensis* are substantially similar to those of *ewerbecki*.

Segments in a midbody annulus 22 (10 + 12), but counts made on only a score of paratypes: annuli on body 263 (252-277 in paratypes, viz. 252-269 in ♂ ♂, 261-277 in ♀ ♀) of which

the median pair of ventrals are *only* about 1½ times as broad as the adjacent ones; annuli on underside of tail *from* post-anal ring to conical tip 27 (22-26 in 37 paratype ♂♂, 22-25 in 42 ♀♀); anals 6 (4 in four paratypes, due to fusion), the median pair much enlarged, the immediate flanking pair of laterals entire, transversely divided, or reduced to a tiny wedge

Color. In alcohol. Grayish white (? flesh-pink in life), uniform except that much of the tail, both above and below, may be purplish.

Size. Total length of holotype ♂, 160 (143 + 17) mm., largest of the 38 ♂♂; largest ♀ (I 9250), 170 (153 + 17) mm.

Total length of smallest ♂, 124 (111 + 13) mm., of smallest ♀, 100 (90 + 10) mm.

In the 38 ♂♂ the tail is included in the total length from 8.7 to 10.1 times, average 9.4 times; in the 62 ♀♀ from 9.4 to 10.9 times, average 10.1 times.

BREVIORA

Museum of Comparative Zoology

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NOTES ON THE HERPETOLOGY OF HISPANIOLA.

7. NEW MATERIAL OF TWO POORLY KNOWN ANOLES: *ANOLIS MONTICOLA* SHREVE AND *ANOLIS CHRISTOPHEI* WILLIAMS.

BY ERNEST E. WILLIAMS

Recent expeditions in Haiti have obtained material of two anoles, one of which (*A. monticola* Shreve) had been previously recorded on the basis of the unique type specimen, and the other (*A. christophei* Williams) was known only from type and paratype.

Examination of the new material suggests that the two species, though in a number of respects strikingly different, may yet be related. It is, therefore, appropriate to discuss these two species jointly. Comparison is made also with *Anolis darlingtoni* Cochran = *A. etheridgei* new name,[1] regarded by Cochran (1939, 1941) as allied to *monticola*.

ANOLIS MONTICOLA

A. monticola Shreve 1936 was described from a single male (lacking most of the tail and darkened by formaldehyde) collected by P. J. Darlington in "the northern and eastern foothills, Massif de La Hotte, 1000-4000 feet, Haiti."

No other specimens have been reported since the original description. However, specimens had been collected for the American Museum of Natural History by W. G. Hassler in 1935 in the vicinity of Aux Cayes and Camp Perrin. These, like the type, are in a dark phase and show only the faintest trace of pattern. In Hassler's notebook, on the other hand, there

[1] Etheridge (unpublished thesis, University of Michigan) has shown that the genus *Xiphocercus* cannot be retained. Thus, *Xiphocercus darlingtoni* Cochran 1935 joins the genus *Anolis*, and *Anolis darlingtoni* Cochran 1939 must in consequence be renamed. I propose, with Miss Cochran's kind consent, that the later named species be called *Anolis etheridgei*.

is an excellent description of colors in life. The American Museum specimens (as well as Hassler's notes) were examined by Max Hecht some years ago and the material tentatively referred to *monticola* Shreve.

In 1960, A. S. Rand and J. Lazell (collecting in Haiti with the aid of a grant from the American Philosophical Society) returned with the first well-preserved specimens of this very beautiful small lizard.

A. S. Rand reports the circumstances under which this material was collected as follows:

"The *monticola* were found along the trail one-half day's ride above Camp Perrin. The trail there ran along a hillside mostly cut over and grown up to dense bushes and grass. Along this trail were many *hendersoni* subsp. in the bushes, particularly where they were shaded by occasional trees. I remember also seeing *cybotes* and one *ricordii*.

"At one point we came to a small patch of rocks . . . boulders of various sizes, some very large, heaped one on top of another a bit like but less extreme than the boulder heaps in the Panduras Mts. in Puerto Rico. This area had not been cleared and growing up from among these boulders were sizeable trees and much smaller woody vegetation. The result was a dense, heavily shaded patch of bush isolated in an open sunny area. It was in this spot on the trees, bushes, fallen branches among these large boulders that we found the *monticola*."

The available sample of *Anolis monticola* now consists of the following specimens:[1]

Haiti. Department du Sud. *Northern and eastern foothills, Massif de La Hotte, 1000-4000 ft.:* MCZ 38296 (type). *Mountains 25 miles north of Aux Cayes on Jeremie Road:* AMNH 49818, 49845, 50108-9, MCZ 56139 (formerly AMNH 50110). *In mountains on road to Jeremie about 8 miles from Camp Perrin, 2000-3000 ft.:* MCZ 56140 (formerly AMNH 50097). *Tombeau Cheval between Camp Perrin and Beaumont:* MCZ 62998-63007. *Grande Cayemite:* MCZ 58026.

The last specimen requires special discussion. It is the Everdam specimen (formerly MCZ 25483B) discussed by Miss Cochran (1941, p. 179) as a juvenile *coelestinus* with keeled ventral scales. Though like many Everdam specimens poorly

[1] Museums from which specimens are cited in this paper are abbreviated as follows: AMNH, American Museum of Natural History; MCZ, Museum of Comparative Zoology; UMMZ, University of Michigan Museum of Zoology.

preserved and dried, it seems a typical *monticola* with the characteristic swollen middorsals as well as keeled ventrals. It is important in extending the range of *monticola* to this small island off the north coast of Haiti's southwestern peninsula. Hassler's and the more recent collection were all made in a relatively small area in the southeastern foothills of the Massif de La Hotte. However, the type, like the Grande Cayemite specimen, came from north of the Massif de La Hotte. (Recent evidence, still unpublished, indicates that there may be striking differences between the forms to the north and to the south of this ridge.)

The new specimens show that the species reaches at least 46 mm snout-vent length.

Color notes and sketches are available for *A. monticola* both from W. G. Hassler and from the Rand-Lazell expedition.

Hassler's color notes are for specific specimens:

1. *Male* (Field no. 74, now AMNH 49845). General dorsal color Hooker's Green. Saddles brown green, three in number, narrowest middorsally, one across shoulder, two between fore and hind legs. A light crescent in the temporal region. Throat and belly dark olive green. Legs barred. Tail barred. Eyes Antwerp Blue, sometimes changing to greenish. Edge of orbit yellowish brown. Skin of fan (which is relatively small) blue, scales light and dark green. Occurring also in a dark phase almost without pattern.

2. *Female* (Field no. 70, AMNH 50097 = MCZ 56140). Back brownish, bounded laterally by a wavy reddish line edged with a dark line. Sides below the dark line olive shading to very light yellowish green. Sides of neck yellowish green. Tail nearly plain brown. Legs reddish brown posteriorly. Belly nearly white. Upper lips bluish. Throat yellowish with some green.

I have examined also by courtesy of Mr. Hassler (now of the Fort Worth Children's Museum, Fort Worth 7, Texas) a color sketch, made by Melville P. Cummin, of the head and neck of a live male from "mountains on Jeremie road about 30 miles from Cayes, 2000-3000 ft. alt., August 28-29, 1935." This shows very well the blue of the chin and the yellow green ground color of occiput and nape as well as the black white-centered ocelli which occur laterally on the occiput and nape of some male specimens.

Hassler's photographs of a live male and a female contrast the ocelli and the strong banding of the body in the male with the almost patternless female.

The observations of Rand and Lazell are in excellent agreement with those of Hassler. A pencil and crayon sketch from life is included in their field book and Lazell's description of the same specimen, now MCZ 63004, may be paraphrased as follows:

Ground color yellow green, top of head darker. Body banded with velvety black. Upper and lower jaws blue, this color continued as a stripe fading to whitish above shoulder. An area behind the eye and a V-shaped band across the neck ochre yellow. In the black mark on the neck behind the yellow is a long, thin sky-blue spot. Another such blue spot in the black area on the occiput and anterior to it, still within the black area, a larger white spot with a pale pink center. Legs banded, with a brownish wash. Venter and fan bright yellowish green, but base of fan with a bluish wash on both scales and skin.

Lazell comments (in agreement with Hassler) that the males can turn very dark after capture, obscuring the markings to an extreme degree, such that only the markings on head and neck are still visible, but the jaws always retain their bluish color and the fan its bright yellow green with a blue wash. (The type was apparently preserved in this phase; no markings at all are visible, but the blue of the chin remains evident.)

All the males in the Rand and Lazell collection have two prominent pairs of ocelli, one on the occiput, one on the nape. In the figured specimen the light spots in the interior ocelli are divided. In the preserved specimens the light zone between the two pairs of ocelli may be lighter than the ground color or not. (This is one of the areas described by Lazell as ochre yellow in life.) Banding on body and limbs is always conspicuous; on the flanks each dark band is divided by a lighter, narrow, vertical streak.

The two females obtained by Rand and Lazell show the lighter mid-dorsal zone bounded by a wavy dark line mentioned by Hassler. Rand, who has described these specimens, cites the color of the middorsal zone as greenish brown. The inward curves of the dark line are gentle, the convex portions of the line are produced into points by larger or smaller spots of color even lighter than the broad middorsal zone. There is blue on the sides of the chin, and the throat is green and the belly whitish in life.

Anolis christophei

The species *A. christophei* Williams 1960 was based on two female specimens obtained in the vicinity of La Citadelle of

King Christophe, one collected by W. J. Eyerdam for the Museum of Comparative Zoology in 1927, and one collected by W. G. Hassler for the American Museum of Natural History in 1935.

A series of this species, including the previously unknown males, has now been secured again in the vicinity of the Citadelle by Luc and George Whiteman collecting for the Museum of Comparative Zoology as part of a collecting program in Haiti partly supported by N.S.F. grant G 16066. Unfortunately these are without notes on color in life or any record of dewlap color. They are recorded as occurring on walls and on the ground.

The type (MCZ 25485) and paratype (AMNH 49736) are now supplemented by the following specimens (all from La Citadelle):

MCZ 66900-19, UMMZ 122818(5).

The color as ascertained from preserved specimens is not very different from that described by Cochran (1941) for the type, as quoted in the original description.

Male. Snout mottled. Two dark supraorbital stripes, neither sharply defined, the posterior stripe coalescent with an arc of dark pigment surrounding a light area which encloses the interparietal. A scalloped, crescent-shaped transverse dark mark on the occiput. A butterfly-shaped mark middorsally in front of shoulder, light-edged behind. Three similar marks between the fore and hind limbs and above the sacrum, but in each of these the anterior margins are ill defined. Tail indistinctly banded.

On each side a light line from the ear arching downward to join a dark-edged light line just above root of arm, continuing halfway along the body. Flanks above and below light line strongly mottled with darker. Limbs mottled light and dark.

Labials above and below darkly pigmented. Venter washed and powdered, with throat and undersides of limbs and tail darker, with some obscure light spotting, least evident on the throat. Dewlap scales white, skin grey.

Female. Pattern as far as discernible the same but much more obscure. Throat and limbs more distinctly spotted with white.

Even in the male the pattern, while complex and distinct, is not prominent. Near hatchlings show the same pattern especially well-defined, but even in these the contrast of dark and light areas is not really bold or striking. In all cases specimens must be fully immersed in liquid before the pattern becomes at all evident.

COMPARISON OF A. CHRISTOPHEI, A. MONTICOLA AND A. ETHERIDGEI

A. monticola, A. christophei and *A. etheridgei* are all small anoles (44-48 mm snout-vent length) of, as far as known, quite local distribution. (See map.)

Only *A. etheridgei* is known to be montane, reaching at least 6000 feet elevation. *A. monticola*, despite its name, is not known above 3000 feet, and *A. christophei* is known only from the Citadelle which is not more than 2000 feet high.

All three belong to the set of Hispaniolan anoles that have the ventral scales arranged in transverse rows. They differ from all other Hispaniolan anoles (except the very different giant anole *A. ricordii*) in having the subocular scales separated from the supralabials by a row of intervening scales. In the other Hispaniolan anoles the suboculars and supralabials are in contact.

The three species share other minor details of squamation: 10-14 scales across the snout; 6-7 loreal rows; 6-7 supralabials to center of eye; temporals and supratemporals finely granular; interparietal smaller than ear; only one sublabial in contact with the infralabials; lamellae under phalanges ii and iii of fourth toe 14-19.

They are somewhat similar also in basic color pattern. All have the dorsum transversely marked. In *monticola* the dorsal

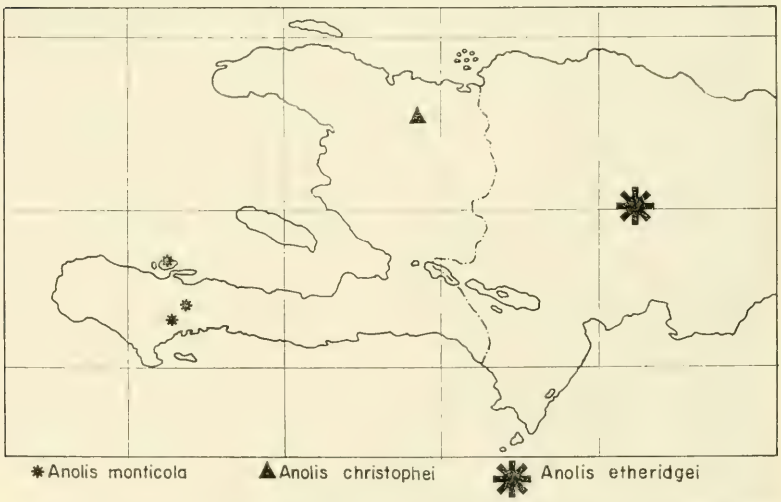

Figure 1. Map of the distribution of *Anolis monticola, A. christophei* and *A. etheridgei* on Hispaniola.

marks extend on to the flanks as transverse bands; in *christophei* and *etheridgei* they are restricted to the dorsum as saddle-like markings and in *etheridgei* rather broken up into mottling.[1] *Monticola* is strongly sexually dimorphic in pattern; *etheridgei* weakly so; *christophei* hardly so at all.

In spite of all resemblances, however, we deal with three strongly marked species, almost as distinct from each other as from other Hispaniolan anoles.

Table I compares the differences in squamation between the three taxa.

As Cochran suggested in the description of *darlingtoni* (= *etheridgei*), this species seems the closest relative of *monticola*. *Christophei* in its lack of the specializations of the other two forms — in particular, in its possession of a well-developed dewlap — seems the most primitive of the trio.

The bright bold patern of male *A. monticola* would seem *prima facie* an obvious compensation for the extreme reduction of the dewlap, which is in most species a striking species-recognition mark. We do not have a description of colors in life of *A. etheridgei*; it would be reasonable to expect a more vivid pattern than appears on the available specimens. We also lack adequate information on the color in life of *christophei*. In regard to the latter species I can only state that the material recently received and in a state of preservation that normally retains well any vivid pattern seemed nondescript and obscurely patterned until very closely examined.

Whether there are any more members of this small sub-group of Hispaniolan anoles will have to be determined by more thorough search of the island. *A. etheridgei* is still known only from four localities in the Cordillera Central of the Dominican Republic (Loma Vieja, Loma Rucilla, Valle Nuevo, Constanza), *A. monticola* from four localities in the foothills of the Massif de La Hotte and on the island of Grand Cayemite, and *A. christophei* only from the single locality, the vicinity of La Citadelle. These are widely separated areas. If related species are equally local in distribution, they may well have been missed. Of course, we lack at the moment any information which would permit significant hypotheses on the history of these forms. There is indeed evidence that suggests that these three forms are one branch of an extremely interesting intra-Hispaniolan radiation; this conception, however, will be documented in another paper.

[1] I rely on Miss Cochran's description of *A. darlingtoni* = *etheridgei* for evidence of transverse, dorsal, saddle-like markings in this form. At the time of writing twenty years later they are not at all evident on the specimens.

TABLE I

Comparison of Squamation

monticola	*christophei*	*etheridgei*
10-12 scales across snout	10-12 scales across snout	13-14 scales across snout
scales in frontal depression numerous, *elongate, keeled*	scales in frontal depression numerous, *hexagonal* or *round*, smooth	scales in frontal depression numerous, *subhexagonal, keeled*
supraorbital semicircles separated by 3 scales, the median smaller	supraorbital semicircles separated by 1-2 scales	supraorbital semicircles separated by 3 scales, equal in size
anterior canthal scales *not* abruptly smaller than posterior	anterior canthals *abruptly* smaller than posterior	anterior canthals *not* abruptly smaller than posterior
posterior frontal *ca.* ⅔ size anterior supraocular	posterior frontal *ca.* ⅓ size of anterior supraocular	posterior frontal *ca.* = very small anterior supraocular

TABLE 1 (Cont.)

mentals wider than long in contact with 4 scales posteriorly between sublabials	mentals longer than wide in contact with 6 scales between sublabials posteriorly (2-4 inserted between the tips)	mentals wider than long in contact with 3 scales between sublabials
2-4 middorsal rows swollen, keeled	2 middorsal rows slightly enlarged (in males only)	no middorsal rows enlarged
ventrals small, keeled, in transverse rows, imbricate, mucronate	ventrals very small, rounded or squarish, in transverse rows, juxtaposed	ventrals small, rounded or squarish, in transverse rows, subimbricate
dewlap vestigial, indicated by a slight longitudinal fold, scales small, keeled	dewlap extensive, prominent with rows of 3-4 smooth scales smaller than ventrals separated by areas of naked skin (except at edge where scales are longer than ventrals, cycloidal, imbricate	dewlap vestigial, indicated by a longitudinal fold, scales small, smooth

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Figure 2. *Anolis monticola* Shreve, MCZ 63004.

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. AUGUST 22, 1962 NUMBER 165

AN EXTINCT SOLENODONTID INSECTIVORE FROM HISPANIOLA

By Bryan Patterson

During the summer of 1958, Drs. Clayton E. Ray and A. Stanley Rand carried on field work[1] for this museum in Puerto Rico and the Dominican Republic. Particular attention was paid to cave deposits, and a number of previously unexplored caves were examined. The cave containing the material reported on here is in the Sierra de Neiba near Rancho La Guardia in the Province of San Rafael, Dominican Republic; it has no local name. Situated in a limestone cliff and accessible only by a nearly vertical climb of some 30 feet, the cave contains a number of chambers connected by narrow passages.

Bones were encountered in the deposits on the floor of the antechamber and of the first chamber beyond it. In the antechamber two layers are present, an upper, dark grey to black one some six inches thick, and a lower, reddish-brown one eight to ten inches in depth. The upper layer is either lacking or negligible in depth in the first chamber, the lower there attaining a thickness of six to twelve inches. Scanty remains from the upper dark layer include *Rattus*, which clearly indicates post-Columbian age. No introduced forms were encountered in the reddish-brown layer, which contains indigenous rodents and the three species of *Nesophontes*[2] known to have inhabited the island, together with scanty remains of bats, birds, lizards, and solenodontids. In addition to the bones of the extinct form described below, one specimen of *Solenodon paradoxus* was obtained. This is the left horizontal ramus of a young individual

[1] Partly supported by a Sigma Xi-RESA grant-in-aid.

[2] *N. paramicrus, hypomicrus* and *zamicrus* of Miller (1929). *N. "paramicrus,"* the largest of the three, agrees in size with the Cuban *N. micrus*, from which Miller separated it on molar characters. I have examined several hundred specimens of the Hispaniolan form and compared them with Cuban material. The supposed differences are not constant and I have so far been unable to find others that might validate Miller's species.

with I_2 in process of eruption and alveoli of the other teeth (M.C.Z. no. 7260); as far as I am aware this find constitutes the first fossil (or subfossil) record of the species. Judging from the good preservation and completeness of most of the bones from the reddish-brown layer, Dr. Ray (MS field notes) is inclined to doubt that their occurrence is a result of owl-roost accumulation. Most of the material, including all the solenodontid remains, was found in the first chamber of the cave. As regards the age of the layer, all that can presently be said is that it is almost surely pre-Columbian.

During their stay in the Dominican Republic, Drs. Ray and Rand were accompanied by Professor Eugenio de Jesús Marcano F., Universidad de Santo Domingo, whose aid was invaluable in all phases of the work. It is a pleasure to name the extinct solenodontid in his honor. Dr. Ray will discuss the rodents from this and other localities in the course of his comprehensive studies on the Antillean Rodentia. I am indebted to Miss Linda Loring for the cleaning, sorting and cataloguing of the other groups represented in the collection. The drawings are by Mrs. Dorothy Marsh. I have been fortunate indeed as regards comparative material, thanks chiefly to the excellent series of *Solenodon* in the Mammal Department of the museum. Thirty-six mandibles, fifteen humeri and six ulnae of *S. paradoxus* and three mandibles of *S. cubanus* have been available. I have not seen limb bones of *S. cubanus*, but published figures (e.g. Peters 1863) indicate that these do not differ appreciably, either in structure or in proportions, from those of the larger species.

INSECTIVORA

SOLENODONTIDAE

Antillogale[1] gen. nov.

Type: — *A. marcanoi* sp. nov.

Distribution: — Quarternary, Hispaniola.

Diagnosis: — Differing from *Solenodon* as follows: P_4 and lower M smaller relative to size of jaw, lower M with lingual cleft between paraconids and metaconids deeper, paraconid wings directed more anteriorly, paraconids consequently farther from metaconids, low ridge between bases of paraconids and metaconids isolating slight valleys at bases of trigonid basins, anterior

[1] The Antilles, plus γαλή, weasel.

cuspules below bases of paraconids very weakly developed, heels less broadly shelf-like labially. Post-dental portion of ramus larger relative to anterior portion. Humerus and ulna shorter, much wider relative to length, ulna with pit proximo-medial to sigmoid notch.

Antillogale marcanoi sp. nov.

Type: — M.C.Z. no. 7261, incomplete right ramus of mandible with P_3-M_2 and alveoli of other teeth.

Hypodigm: — Type and the following specimens: M.C.Z. nos. 7262, incomplete left ramus with P_4-M_2 and alveoli of P_3, M_3; 7266, posterior portion of left ramus with alveoli of M_3, juvenile; 7263, right humerus lacking ectepicondyle; 7264; left humerus lacking proximal epiphysis; 7265, right ulna.

Horizon and locality: — Late Pleistocene or Recent; unnamed cave 2 kilometers SE of Rancho La Guardia, Municipio de Hondo Valle, Provincia de San Rafael, República Dominicana.

Diagnosis: — As for the genus.

Description: — Knowledge of the lower incisors, canine and anterior premolar derives solely from alveoli. On this evidence, the relative sizes of the incisors and the degree of enlargement of I_2 were essentially as in *Solenodon*, as was the relative size of the single-rooted canine. The anterior premolar would appear to have been larger than P_3, to about the degree seen in *S. paradoxus*. P_3 is small relative to P_4, nearly as much so as in *S. paradoxus*, and much smaller, both actually and relatively, than in *S. cubanus*. In structure it is very similar to the corresponding tooth of *S. paradoxus*, and rather different from the larger, more globular one of *S. cubanus*. The paraconid of P_4 is a larger cusp than in the majority of specimens of *S. paradoxus* and much larger than in *S. cubanus*. The essential characters of the molars have been given in the diagnosis and can be seen in the figures: I may add that, as far as these teeth are concerned, *Antillogale* could only with difficulty be distinguished generically from *Apternodus*.

The horizontal ramus is shorter and more slightly built than in *Solenodon* and, instead of the two, or even three, mental foramina almost invariably present in that form, there is only a single large one, situated beneath P_3. The postdental portion of the mandible is relatively large and robust. Whereas the horizontal ramus is rather shorter than in *S. cubanus* the posterior part is rather larger and longer, being intermediate in

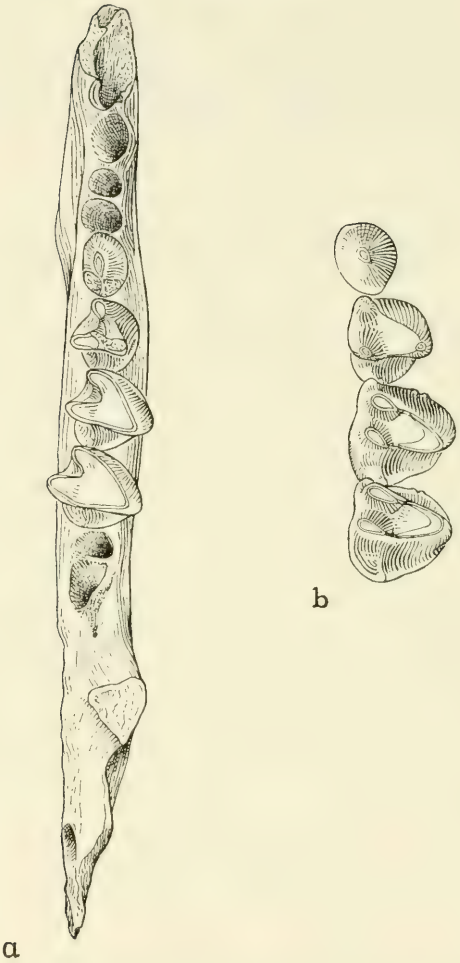
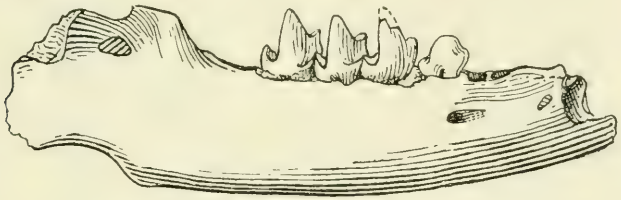


Figure 1. a) *Antillogale marcanoi*, type, M.C.Z. no. 7261, incomplete right ramus, dorsal view. b) *Solenodon paradoxus*, M.C.Z. no. 12384, crown view of right P_3-M_2. × 3.

these respects between *cubanus* and *paradoxus*. The coronoid process, so far as can be judged from the juvenile M.C.Z. 7266 and the incomplete M.C.Z. no. 7262, appears to have been less tapering than in the living species. The base of the anterior border of the process is convex, as in *S. cubanus*, and not excavated as it is in *S. paradoxus*. The masseteric fossa is small,

relatively and actually, oval in outline, and not very sharply defined. The marginal process, for the insertion of M. digastricus, is comparable to those of the living forms. The angle is not complete in any of the specimens but enough is preserved in M.C.Z. no. 7262 to demonstrate that, in contrast to *S. paradoxus* and in agreement with *S. cubanus*, the ventral border is not



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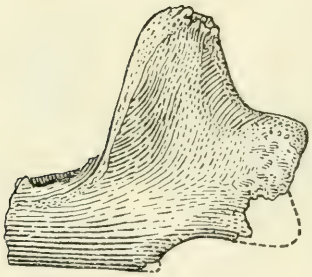

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Figure 2. *Antillogale marcanoi.* a) M.C.Z. no. 7261, type, incomplete right ramus, lateral view. b) M.C.Z. no 7266, incomplete left ramus, lateral view, × 2.

downcurved and that, consequently, there is no lunate notch between angle and marginal process.

The limb bones differ markedly in proportions from those of *Solenodon*. The humerus of *Antillogale* may be summed up as a bone having the width but not the length of that of *S. paradoxus*, and hence massive. The relative lengths of humerus and ulna appear to be essentially the same in both. The ulna, like

the humerus, is shorter than but equally as wide as that of the living species; other differences of note between the two are the presence in the fossil of a very distinct pit proximo-medial to the sigmoid notch and of a rugose interosseous border.

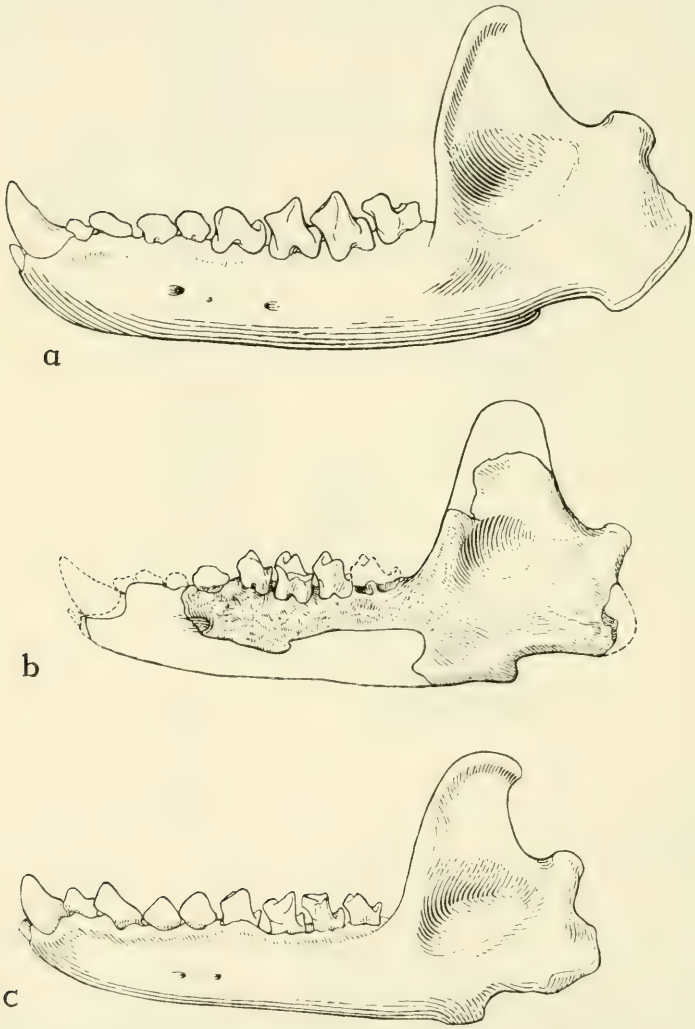

Figure 3. Lateral views of left rami of a) *Solenodon paradoxus*, M.C.Z. no. 34828, b) *Antillogale marcanoi*, M.C.Z. no. 7262, and c) *Solenodon cubanus*, Y.P.M. no. 1203. In b) areas in solid outline are restored from M.C.Z. nos. 7261 and 7266. × 3/2.

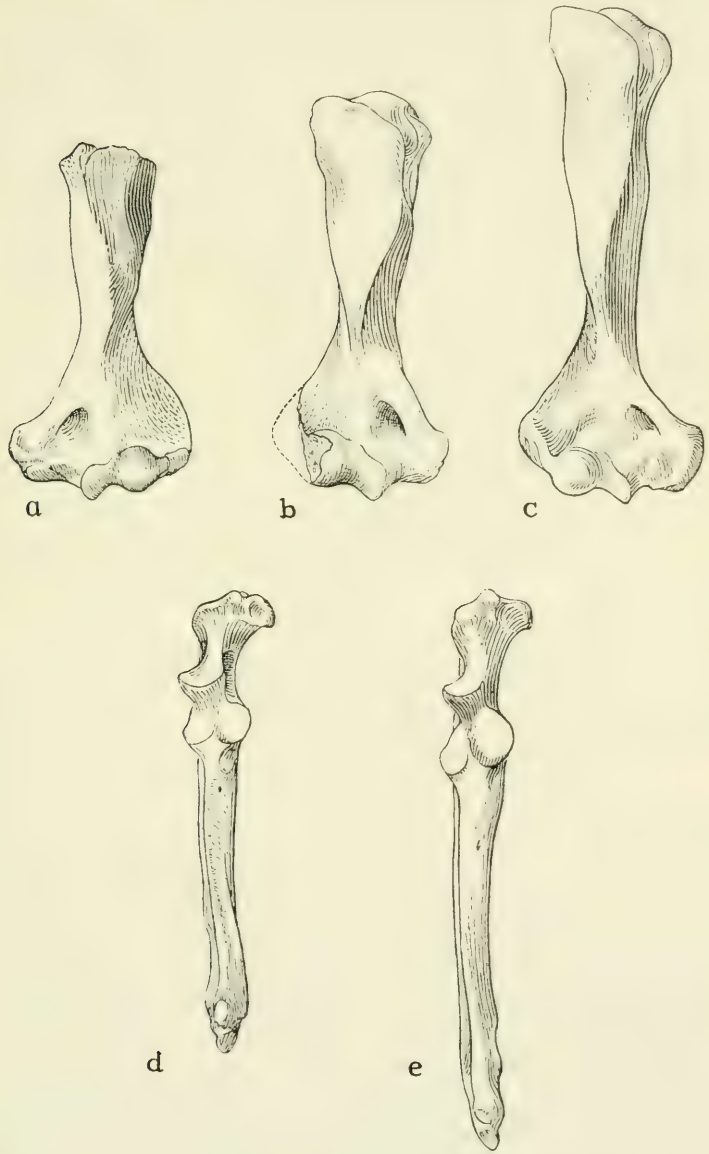

Figure 4. Anterior views of humeri (a-c) and ulnae (d, e). *Antillogale marcanoi,* a) M.C.Z. no. 7264, b) M.C.Z. no. 7263, d) M.C.Z. no. 7265. *Solenodon paradoxus,* c) and e) M.C.Z. no. 12416. × 4/3.

Measurements in mm.

	M.C.Z. nos.	
	7261	7262
P_3, length	2.7	—
width	2.0	—
P_4, length	3.1	3.2
width	2.3	2.5
M_1, length	3.0	3.4
width	2.9	—
M_2, length	3.3	3.4
width	3.0	3.3
Depth of ramus beneath M_1	6.5	—
	7263	7264
Humerus, total length	40.0	—
a.-p. diameter of proximal end	9.9	—
tr. diameter of proximal end	10.9	—
a.-p. diameter at center of shaft	7.1	6.6
tr. diameter at center of shaft	7.3	6.5
a.-p. diameter of distal end	5.1	4.9
tr. diameter of distal end	—	17.7
tr. diameter of trochlea	—	9.2
	7265	
Ulna, total length	45.6	
a.-p. diameter of olecranon	4.8	
tr. diameter of olecranon	7.4	
tr. diameter of proximal articular surface	6.4	
a.-p. diameter at center of shaft	4.3	
tr. diameter at center of shaft	2.3	
a.-p. diameter at distal end	3.9	
tr. diameter at distal end	2.8	

Discussion: — The Solenodontidae have thus far been known from one genus with two species. Splitting of these taxa has of course been attempted. *Solenodon cubanus* has been made the type of *Atopogale* by Cabrera (1925), and Barbour (1944) has described a second Cuban species, *S. poeyanus*, based on pelage characters. Barbour explicitly stated that he could detect no cranial or dental distinctions. Aguayo (1950) and Koopman and Ruibal (1955) have regarded this form as a subspecies of *cubanus*. The latter authors noted that some fragmentary remains (M.C.Z. no. 7054) from a cave in Camaguey, which they referred to the living species, were somewhat larger than Recent specimens of *cubanus* examined by them. In recent years, members of the Sociedad Espeleológica de Cuba have obtained further material, including some skulls, from the Province of Havana. Thanks

to Sr. Oscar Arredondo, I have seen most of these specimens; they also represent individuals rather larger than, although not otherwise different from, any in the small sample (3) of *cubanus* available to me. It is of some interest that the type of *poeyanus* (M.C.Z. no. 6957) is also rather larger than this sample, a point not mentioned by Barbour; in fact there is agreement in this respect between the type and these fossils (or subfossils). To conclude from this that *poeyanus* is distinguishable from *cubanus* on the basis of size and that the fossils so far found are referable to the former would, I think, be premature. The available series are too small to rule out accidents of sampling. The size difference is slight and if the size range of *cubanus* is comparable to that shown for *paradoxus* by the adequate series at hand we could be dealing simply with segments of a normal distribution. Reinforcing caution is the fact that one of the two mandibles from Maisi, Oriente (M.C.Z. no. 10065), mentioned by Allen (1918) is smaller than the other fossils. Whatever the solution of this minor problem may prove to be, I agree entirely with Aguayo and with Koopman and Ruibal that subspecies, at most, are involved. There is at present no good evidence of more than one species of *Solenodon* in Cuba. *Atopogale* is recognized, either as a genus or as a subgenus, by some authors. There can be no question that *paradoxus* and *cubanus* are clear-cut taxa but they seem to me, as to others, to merit no more than specific rank. *Antillogale marcanoi* helps to clarify matters here; it is sharply distinct from either of the living species and the latter share most of the characters that differentiate them from it.

Antillogale is quite evidently a member of the Solenodontidae. The structure, although not the proportions, of the known limb bones; the general structure of the mandible, and especially the presence of a marginal process; the small I_1 and the degree of enlargement and mode of implantation of I_2 (as revealed by the alveoli) — all these characters combine to place this conclusion beyond reasonable doubt. Only in lower molar structure is there a closer resemblance to members of another family, the Apternodontidae. The difference here I believe to be the result of specialization in the *Solenodon* phylum. The molars of the two living species give the impression of having undergone anteroposterior compression of the trigonids. A majority of the characters in which they differ structurally from those of *Antillogale* could be directly correlated with such a change. Aside from molar structure, the differences between the extinct and the living species are chiefly of a proportional nature, as

pointed out above. *Antillogale* evidently had a somewhat shorter facial region and much shorter, more heavily built fore limbs than *Solenodon*. It may well have been more fossorial in habits.

Solenodon with its two species, one on each of the larger West Indian islands, has always been one of the most isolated of mammals, zoogeographically — and even taxonomically — speaking. As knowledge of the past history of mammals has improved, this isolation has become, if anything, even more apparent. In earlier days it was at least possible to assume a common ancestry with if not membership in the Tenrecidae. There is now no real evidence for such an assumption — tenrecids, as far as the record goes, appear always to have been African and Madagascan in distribution — and we must look elsewhere for close relatives and possible ancestors. The only group that seems to me to come close to fulfilling the requirements is the Apternodontidae, a family which at least had the merit of inhabiting North America, the only probable source area.[1] The described forms, the Oligocene *Apternodus* and *Oligoryctes*, were certainly not ancestral to the solenodontids, but apternodontids are now known in North America at least as far back as the Bridgerian Eocene.[2] The possibility, I would go so far as to say probability, exists that solenodontids were derived from relatively unspecialized apternodontids that inhabited the Central American peninsula during the earlier Tertiary. Rafting of the ancestral stock to the Antilles, for rafting was certainly involved, may have taken place in the later part of the Eocene, at roughly the same time as the rafting of the ancestors of caviomorph rodents and platyrrhine primates to South America. This event, if it occurred at the time suggested, would have insured for the solenodontids a very long residence in the West Indies. There has, I feel, been some reluctance to accept such a possibility, a reluctance based, consciously or unconsciously, on the fact that *Solenodon* alone has hitherto represented the family and on the assumption that we now have an adequate idea of the Pleistocene, or at least pre-human, faunas of the archipelago. I strongly doubt if we do have a good

[1] Allen's belief (1918) that solenodontids were derived from nesophontids, a view recently supported by McDowell (1958), is not at all convincing. McDowell's attempt to read *Apternodus* out of the Insectivora is utterly unrealistic, being in large part based on misinterpretation of the fossils he examined.

[2] I am indebted to Dr. Craig C. Black for the opportunity of examining a specimen from Tabernacle Butte, Wyoming. This is the earliest known eutherian with zalambdodont molars. Contrary to earlier statements (including one of mine made on the basis of the literature), the molars of the Paleocene *Palaeoryctes* are not zalambdodont in structure, nor are they even pre-zalambdodont in the way those of *Potamogale* are.

knowledge of the faunas (cf. Koopman and Williams 1951); as regards birds at any rate Sr. Arredondo and I will demonstrate the contrary in a forthcoming paper. And now, in *Antillogale*, we have a hint that there may have been a radiation of solenodontids on the Antilles in some degree comparable to that of the tenrecids on Madagascar.

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BREVIORA

Museum of Comparative Zoology

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LECTOTYPES OF SPECIES OF OGCOCEPHALIDAE SELECTED FROM SYNTYPES IN THE MUSEUM OF COMPARATIVE ZOOLOGY

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During the 1891 expedition of the U. S. steamer "Albatross" to the eastern tropical Pacific, about 80 specimens of fishes of the family Ogcocephalidae were taken. Garman, who studied the collection, concluded that it represented twelve species, ten of which were described by him as new (Garman, 1899). The remarkable thing is that subsequent collecting in the same area has produced additional examples of only about half of these species; the rest remain known only from specimens taken on the original expedition.

It became necessary for me to examine this valuable "Albatross" collection in the course of work on the family Ogcocephalidae. Then it was discovered that most of the specimens upon which Garman based his original descriptions had been designated as syntypes, a common practice at the time. In the interest of stabilizing the nomenclature of this group, I have selected lectotypes for the species heretofore represented by syntypes. The list of species below includes only those for which Garman wrote original descriptions. They are arranged in the order in which they appear in his paper.

OGCOCEPHALUS PORRECTUS

The original lot contained four specimens from "Albatross" Sta. 3368A, and of these Hubbs (1958) selected the largest specimen as lectotype; it bears the number MCZ 28733. The other three specimens are now removed to MCZ 41594.

[1] This investigation was supported by Public Health Service Fellowship No. 8543 from the Division of General Medical Sciences, Public Health Service.

Halieutopsis tumifrons

The only two specimens known of this species are those originally taken by the "Albatross." It was not possible for me to determine which of the two had been figured by Garman, so the choice of a lectotype was arbitrarily made, the two examples being closely similar. The lectotype, MCZ 28729, is from "Albatross" Sta. 3400A. The second specimen, from "Albatross" Sta. 3413A, bears the number MCZ 28730.

Dibranchus hystrix

Garman assigned three examples to this species, and from these I have chosen the specimen that appears to be the one illustrated in the original description; therefore the lectotype is MCZ 28726, "Albatross" Sta. 3375A. The other two specimens are: MCZ 28727, "Albatross" Sta. 3392A, and MCZ 28728, "Albatross" Sta. 3362A.

Dibranchus scaber

Two specimens represented this species originally, the larger of which is apparently that figured in the original description. It has the number MCZ 28724, "Albatross" Sta. 3431A, and is hereby designated the lectotype. The second specimen, MCZ 28725, "Albatross" Sta. 3364A, is a specimen of *Dibranchus hystrix*, not *Dibranchus scaber*. The lectotype of *Dibranchus scaber* is therefore the only known specimen of the species.

Dibranchus asper

This species was described from a single specimen, MCZ 28723, "Albatross" Sta. 3418A; accordingly this specimen is the holotype. My own studies show *Dibranchus asper* to be the same as *Dibranchus hystrix;* of the two nominal species, I hereby place *Dibranchus asper* in the synonymy of *Dibranchus hystrix* for the reason that no figure accompanies the description of *Dibranchus asper*.

Dibranchichthys nudivomer

Altogether, two lots totalling seven specimens represent this species. A specimen in relatively good condition from MCZ 28719, "Albatross" Sta. 3353A, was selected as the lectotype; there was one other specimen in the lot with the lectotype, and

it is now removed to MCZ 41595. The second lot of five specimens bears the number MCZ 28718, "Albatross" Sta. 3395A. These, along with an eighth example from "Albatross" Sta. 3395A which had been sent to the U. S. National Museum (USNM 57867), are the only known specimens of this species.

Malthopsis sparsa

Garman originally assigned three lots totalling 19 specimens to this species. Of these it is impossible to tell exactly which example was used for the illustration in the original description, and the lectotype was chosen more or less arbitrarily from a series considered to be in good condition and which most resembled the original illustration. The lectotype, MCZ 28717, bears a tag indicating that it came from "Albatross" Sta. 3386A, but the situation is not so clear with respect to most of the specimens that were originally in the same lot with the lectotype. Of these there are eight specimens as follows: two specimens with the same station number as the lectotype, i.e., "Albatross" Sta. 3386A; one specimen tagged "Albatross" Sta. 3354A; five specimens with no tags and no indication in the original description as to whether they came from station 3386A or 3354A. These untagged specimens *together* with those from station 3386A are now removed to MCZ 41596. The specimen from "Albatross" Sta. 3354A is certainly an example of *Malthopsis spinosa*, not *Malthopsis sparsa*, and is now removed to MCZ 41597.

The remaining two lots of *Malthopsis sparsa* stand as follows: MCZ 28715, "Albatross" Sta. 3396A, six specimens; MCZ 28716, "Albatross" Sta. 3385A, four specimens.

Malthopsis erinacea

From the original series of eight, the one specimen that appears to have been used for the illustration accompanying the original description is hereby designated the lectotype; it bears the number MCZ 28712, "Albatross" Sta. 3402A. A second specimen originally in the same lot with the lectotype is now removed to MCZ 41598. The other six specimens bear museum numbers as follows: MCZ 28711, "Albatross" Sta. 3358A, one specimen; MCZ 28713, "Albatross" Sta. 3425A, one specimen (this is probably not a specimen of *Malthopsis erinacea*, but it

is small and difficult to place at this time without more comparative material); MCZ 28714, "Albatross" Sta. 3418A, four specimens (these four are actually examples of *Malthopsis spinosa*, not *Malthopsis erinacca*).

Malthiopsis spinosa

Two rather similar specimens were assigned to this species by Garman, but I am unable to tell which was used for the illustration accompanying the original description. I have selected MCZ 28710, "Albatross" Sta. 3392A, as the lectotype. The remaining specimen from "Albatross" Sta. 3393A, originally with the same museum number as the lectotype, is now removed to MCZ 41599.

Malthopsis spinulosa

From a series of 21 specimens from "Albatross" Sta. 3394A, I have selected a specimen on the basis of its similarity to the illustration used with the original description and the fact of its relatively good condition. This specimen bears the number MCZ 28709, and the remaining 20 specimens of the lot are removed to MCZ 41600. From my own examination of this material in conjunction with newer collections, I must conclude that *Malthopsis spinulosa* is the same as *Malthopsis spinosa*. Inasmuch as the original descriptions of both nominal species are accompanied by illustrations of equal quality, I give preference to *Malthopsis spinosa* as the name to represent this taxon by virtue of its page priority. Thus, *Malthopsis spinulosa* falls into the synonymy of *Malthopsis spinosa*.

I am extremely grateful to Mrs. Myvanwy Dick and to Dr. Giles W. Mead, who both took great trouble to assist me in the loan of material.

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BREVIORA

Museum of Comparative Zoology

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Bathyclupea schroederi, a New Bathyclupeid Fish from the Western Tropical Atlantic

By

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The species described below is based on specimens collected by the *Atlantis* during the Harvard-Havana Expedition to Cuba, and by the *Oregon* (exploratory vessel of the U.S. Bureau of Commercial Fisheries) during her work in the Gulf of Mexico. To Mr. Harvey R. Bullis, Jr., director of the *Oregon*'s program, go my thanks for representatives of both western Atlantic species of *Bathyclupea*. I am also indebted to Mr. Loren P. Woods of the Chicago Natural History Museum, and to Dr. Leonard P. Schultz, U.S. National Museum, for the loan of comparative specimens of related species and for additional representation of the new form.

BATHYCLUPEA SCHROEDERI, new species

Holotype: A specimen 140 mm. in standard length, taken at *Atlantis* Station 2987, 23°23′N., 79°39′W., 280 fathoms. MCZ 41498.

Paratypes: MCZ 39416, 4 specimens, *Atlantis* Station 2987, 23°23′N., 79°39′W., 280 fms.; MCZ 39380, 1 specimen, *Atlantis* St. 2987a, 23°22′N.; 79°39′W., 260 fms.; MCZ 40600, 1 specimen, *Oregon* St. 2635, 17°37′N., 63°28′W., 220-235 fms.; CNHM 65145, 1 specimen, *Oregon* St. 1872, 16°41′N., 82°20′W., 300 fms.; CNHM 65147, 1 specimen, *Oregon* St. 1888, 16°41′N., 81°02′W., 250 fms.; CNHM 65146, 1 specimen, *Oregon* St. 1886, 16°55′N., 81°12′W., 275 fms.

Diagnosis: The following species of *Bathyclupea* have been described: *Bathyclupea hoskynii* Alcock, 1891, from the Andaman Sea (the type species); *Bathyclupea argentea* Goode and Bean,

1895, from Nevis, West Indies; *Bathyclupea maylayana* Weber, 1934, from the Flores Sea, Indonesia; *Bathyclupea megaceps* Fowler, 1937, from off Mindanao, Philippines; and *Bathyclupea gracilis* Fowler, 1937, from off Makyan Island, Moluccas.

Bathyclupea schroederi differs from all of these by having a spine and 37 to 39 rays in the anal fin (cf. 33 or fewer). It can also be distinguished from *B. hoskynii* by its less deep body (3.9 to 4.4 in standard length; cf. 3.3), and from *B. argentea* and *B. maylayana* by the placement of the anal fin, which originates in the anterior half rather than in the posterior half. *B. schroederi* can be distinguished from *B. megaceps* by the relative length of the base of its anal fin, which is longer than the head in the new form but shorter in *B. megaceps.* The length of the head in *B. schroederi*, 3.3 to 3.4 in standard length, is shorter than that of *B. gracilis* (3.0 in length).

Description: The description which follows is based on the holotype and paratypes, 120 to 144 mm. in standard length, listed above.

Counts and proportional dimensions are provided in Table 1.

Body laterally compressed, its greatest depth at origin of anal fin, 3.9 to 4.4 in standard length. The dorsal profile is nearly straight. There is a well defined, rather straight lateral line bearing 38 pored scales which are somewhat more adherent than the scales elsewhere on the body. Scales cycloid, deciduous, thin and relatively large. Head naked with large mucous cavities. Vertebrae 10-20-1, total 31.

Head 3.3 to 3.4 in standard length, interorbital flat, 16.3 to 17.1 in standard length. Eye mainly in the posterior half of the head. Nostrils small, contiguous, almost superior. The mouth is nearly vertical. Minute conical teeth on the lower jaw, a single row of minute teeth on the vomer and premaxillary. The anterior end of the vomer protrudes into the mouth, frequently extending forward to beneath the tip of its snout.

There are four gill arches. Moderately long gill rakers, with slight protuberences, on the first and second arches; rakers much reduced and stublike on the third and fourth arches. Gill rakers on the first arch 3 + 16. The gill opening is wide, the branchiostegal membranes free from one another and from the isthmus. Pseudobranchiae present.

The pectoral fin is large, pointed, the upper rays the longest, about 3.5 in standard length. The ventral fins are anterior to the pectorals, short, very slightly separated. The rays are rather

like the ribs of a fan, fitting into a shallow groove when contracted. The dorsal fin originates in the postmedian half of the body, the anal fin in the anterior half.

Color in alcohol: Opercle and abdominal wall dusky. In life the general color was silvery.

It is a pleasure to name this species for William C. Schroeder of the Department of Fishes, Museum of Comparative Zoology, who collected the holotype and several of the paratypes. His many publications, the collecting he has done, and his work in the department have greatly enriched the field of ichthyology.

TABLE 1

Counts, and proportional dimensions expressed in percent of standard length, of the holotype and paratypes of Bathyclupea schroederi.

	MCZ 41498	MCZ 39416	MCZ 39416	MCZ 39416	MCZ 39416	MCZ 39380	CMNH 65145	MCZ 40600	CMNH 65147
Standard length (mm.)	144	144	140	139	137	137	130	120	116
Greatest depth of body (percent)	27.8	26.4	25.0	26.4	25.5	27.0	24.6	25.0	23.3
Greatest depth of body at midpoint	26.4	23.6	25.0	25.0	24.1	24.1	23.1	25.0	23.3
Least depth of caudal peduncle	10.4	9.7	9.3	9.5	9.5	8.7	9.2	9.2	8.6
Greatest width of body	10.4	9.7	7.9	9.5	9.5	8.7	7.7	9.2	7.8
Greatest width of head	12.5	11.8	12.2	12.2	12.4	11.7	11.5	12.5	11.2
Snout to origin of dorsal fin	54.2	55.6	55.0	53.6	54.7	53.2	54.6	50.8	51.7
Snout to origin of anal fin	43.8	43.1	42.8	42.8	45.2	43.8	43.1	47.5	44.8
Snout to insertion of ventral fin	27.8	27.8	28.6	28.6	31.4		26.9	29.2	29.3
Snout to insertion of pectoral fin, ventral angle	28.5	27.8	27.8	29.3	29.9	29.9	26.9	28.0	29.3
Length of base of dorsal fin	10.4	10.4	10.7	10.6	10.9	10.9	10.8	10.0	10.3
Length of base of anal fin	51.4	49.4	47.1	49.3	48.2	51.1	48.4	48.3	50.9
Distance between insertion of ventral fin and origin of anal fin	20.7	20.2	17.8	17.8	20.4		17.7	16.7	17.2
Length of head	28.5	28.5	30.0	29.3	29.2	30.6	27.7	30.0	32.0
Length of snout	8.3	8.3	8.6	8.6	8.7	8.7	8.5	9.2	7.8
Greatest diameter of eye	11.8	11.1	11.4	11.4	11.7	11.7	10.8	11.7	11.2
Width of interorbital space	5.6	5.6	5.0	5.0	5.1	5.1	5.4	5.8	6.4
Length of upper jaw	13.2	13.2	12.2	12.2	12.4	13.1	12.3	12.5	12.9
Counts:									
Dorsal fin	1-9	1-9	1-8	1-9	1-8	1-9	1-9	1-8	1-9
Anal fin	1-37	1-38	1-39	1-37	1-38	1-39	1-38	1-39	1-37
Pectoral fin	1-28	1-28	1-29	1-28	1-28	1-28	1-29	1-28	1-29

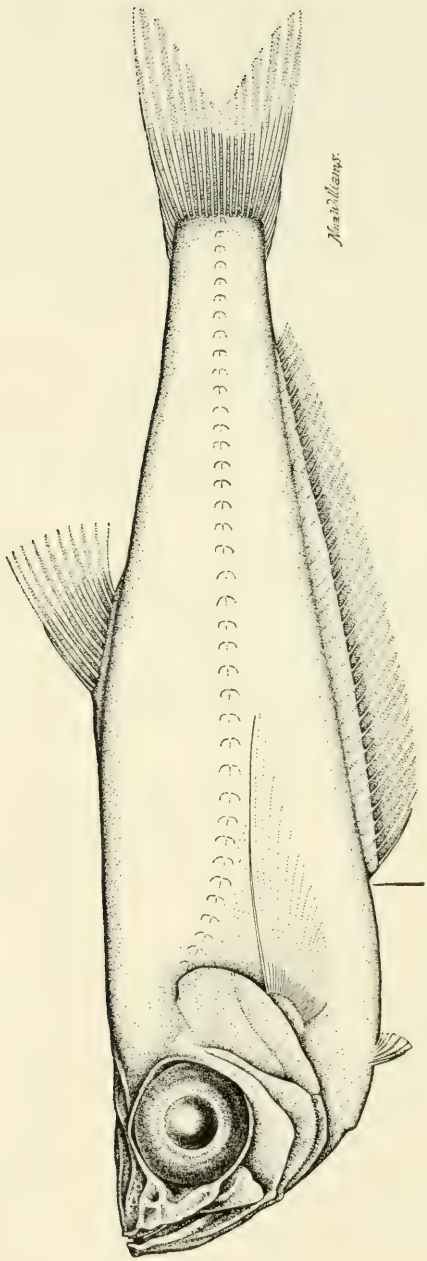

FIGURE 1. *Bathygelupea schroederi*, sp. nov. Holotype, MCZ 41498, from Cuba.

BREVIORA

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TWO NEW SPECIES OF FOSSIL TALPID INSECTIVORES

BY KATHERINE M. REED

During work on the talpid subfamily Proscalopinae, two new scalopine moles came to my attention and are described in this note.

I am grateful to Mr. Richard Tedford, University of California Museum of Paleontology, and Dr. C. W. Hibbard, University of Michigan Museum of Paleontology, for the loan of the material. The work was carried out at the Museum of Comparative Zoology. I am obliged to Professor Bryan Patterson for critical comment and to Miss Barbara Lawrence for access to the collections of Recent insectivores. I also appreciate the comments and assistance of Dr. J. R. Macdonald and Dr. Mary Dawson. The illustrations were made by Mr. Richard Stafford.

The following abbreviations are used:

UCMP—University of California Museum of Paleontology
UMMP—University of Michigan Museum of Paleontology
l., w., trig., tal.—length, width, trigonid, talonid

TALPIDAE

Subfamily SCALOPINAE

DOMNINOIDES Green 1956

DOMNINOIDES VALENTINENSIS n. sp.

Type: UCMP 33152, right ramus with P_1, P_{3-4}, M_{2-3}.

Hypodigm: Type and UCMP nos. 36150-36157, including isolated teeth, partial rami and some limb bones. UCMP 29215 and 29215-A refer to limb material marked "float."

Horizon and locality: Late Miocene, Valentine formation, from the quarries near the middle of the exposed Valentine formation

at the Fort Niobrara locality on the quarter section line between the NW and SW quarters of Sec. 24, T 34 N, R 26 W, Cherry County, Nebraska, UCMP locality V3218 (See Macdonald 1947). The specimens marked "float" are, according to Mr. Tedford, "undoubtedly Barstovian, but come from an undetermined horizon within the Valentine."

Diagnosis: No diastema between P_3 and P_4; slightly larger and more robust than *Domninoides riparensis;* metastylid definite on M_2.[1]

Description: The only upper tooth in the material, and the first known to belong to this genus, is a broken, isolated P^4. This tooth has a blade-shaped paracone. A very narrow anterior cingulum widens to a shelf-like lingual cusp and extends up the posterior side of the tooth to join the paracone crest posteriorly. The lingual cusp is widest opposite the stoutest portion of the paracone. The tooth has at least two, possibly three roots, two labial, one lingual.

In the lower dentition, P_1 is small, conical and single rooted. P_2 is not represented in the material but is double rooted. P_3 is considerably larger than P_1, double rooted as in *D. riparensis*, and with a slight heel. It is situated very close to P_4, with no diastema between these teeth. P_4 is double rooted with a very small anterior cuspule. It has a larger heel than P_3, the heel sloping downwards labially to a small cingulum which connects the heel to the anterior cuspule. The main cusp is conical.

M_1 is not represented in the material studied; thus no comparison with *D. riparensis* is possible in this respect. Relative root sizes are in accord with this species. In M_2 the paraconid is smaller than the metaconid, which is the highest lingual cusp. The entoconid is the stoutest lingual cusp. A crest, the crista obliqua, runs from the hypoconid to the metastylid, as in *D. riparensis*. The protoconid is higher than the hypoconid and is slightly labial to the metaconid. There is a large anterior cingulum, wide labially and with an irregular border, that extends around the paraconid to the opening of the trigonid valley. The posterior cingulum is small and does not reach to the lingual face of the tooth. The talonid has a narrow opening. In M_3 the size relations of the cusps are as in M_2. All examples of this tooth

[1]Dr. J. R. Macdonald has kindly sent me a copy of a forthcoming manuscript in which he describes a new species of *Domninoides*. *D. valentinensis* is distinguished from this species by lacking any trace of cingula on the lingual face of the molars and by the crista obliqua running to the metastylid rather than to the metaconid.

are worn, but there are strong suggestions of a metastylid and of a relatively wide anterior cingulum. No posterior cingulum is present. The talonid is relatively longer than in M_2.

There are usually two mental foramina which vary in position. In UCMP 36151, they are below the anterior roots of P_4 and between P_4 and M_1; in UCMP 33152, between P_{2-3} and the roots of P_4. In UCMP 36152, there is only one foramen, below the anterior root of P_4. In *D. riparensis*, the foramina are below P_3 and between the roots of P_4. The ramus is much like that of *D. riparensis* and is in general similar to that of Macdonald's species, although slightly stouter than in either.

Some comparison of the limb material of the fossil has been made with modern species. It must be noted that the majority of the limb material is "float" and association with the teeth could perhaps be doubted; the extremely talpid-like nature of both does, however, strongly suggest association. The humeri of the fossil are very similar to but slightly smaller than those of *Talpa europaea*. They are larger than in *Parascalops breweri* and wider than in *Condylura*.

Discussion: Macdonald has suggested (pers. comm.) that the jaws of his new species may represent the lower dentition of *Proscalops secundus*. This now seems extremely unlikely, first because of the discovery of P^4 of *Domninoides valentinensis*, which is very unlike that of the Proscalopinae, and second, the greater development of the anterior cingula on lower molars than I would expect on the basis of the known trends in the Proscalopinae (See Reed 1961). Wilson (1960) has recently described lower molars which he assigns to *Proscalops* sp. cf. *P. secundus;* these are much nearer to the proscalopine type of molar than to that of *Domninoides*.

It is evident that *Domninoides* is a talpid, not a soricid as Green (1956) originally described it.

Measurements

UCMP 33152 M_2	UCMP 36152 M_2	UCMP 33152 M_3
l. 3.1 mm	l. 3.2 mm	l. (approx.) 2.4 mm
w. trig. 2.5	w. trig. 2.2	w. trig. 1.9
w. tal. 2.7	w. tal. 2.7	w. tal. 1.6

depth of jaw below M_1, UCMP 33152: 3.7 mm.

Hesperoscalops Hibbard 1941

Hesperoscalops sewardensis n. sp.

Hesperoscalops rexroadi Hibbard 1953, p. 23, fig. 1D.

Type: UMMP 27276, partial right ramus with M_{2-3}, fragment of a left ramus, anterior part of a left ramus with worn M_1, ulna, part of a scapula, and a femur.

Hypodigm: Type only.

Horizon and locality: Late Pliocene or early Pleistocene, from area of Saw Rock local fauna, NE 1/4 Sec. 35, T 34 S, R 31 W, Seward County, Kansas.

Diagnosis: Distinctly larger than *H. rexroadi* and with greater development of basal accessory cuspules.

Description and discussion: The difference in size between the new species and specimens of *H. rexroadi* in which the teeth are in nearly the same state of wear indicates that these cannot be wear differences in the same species and that the two are distinct. Although the cusp pattern is very similar, as Hibbard states (1953, p. 23), the anterior cingular cuspule on M_3 is larger and better developed than in *H. rexroadi,* as is the anterior basal accessory cuspule on M_2. If *Hesperoscalops rexroadi* is ancestral to *Scalopus,* this new, but closely related species must represent an extinct side line, for *H. sewardensis* is considerably larger than *Scalopus aquaticus* and has much better developed basal cuspules and cingula.

Measurements

H. sewardensis

UMMP 27276 M_2		UMMP 27276 M_3	
l.	3.0 mm	l.	2.8 mm
w. trig.	2.5	w. trig.	2.4
w. tal.	2.6	w. tal.	1.7

depth of jaw below M_2 on lingual face: 4.5 mm.
length of M_{2-3}: 5.8 mm.

H. rexroadi

UMMP 27278 M_2		UMMP 27278 M_3	
l.	2.3 mm	l.	2.2 mm
w. trig.	1.9	w. trig.	1.6
w. tal.	2.1	w. tal.	1.5

depth of jaw below M_2 on lingual face: 3.2 mm.
length of M_{2-3}: 5.0 mm.

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PLATE 1

Fig. 1. *Hesperoscalops sewardensis*, UMMP 27276, right ramus, lingual view. 3.75 x.

Fig. 2. *Domninoides valentinensis*, UCMP 33152, crown view of left ramus; stereoscopic pair. 3 x.

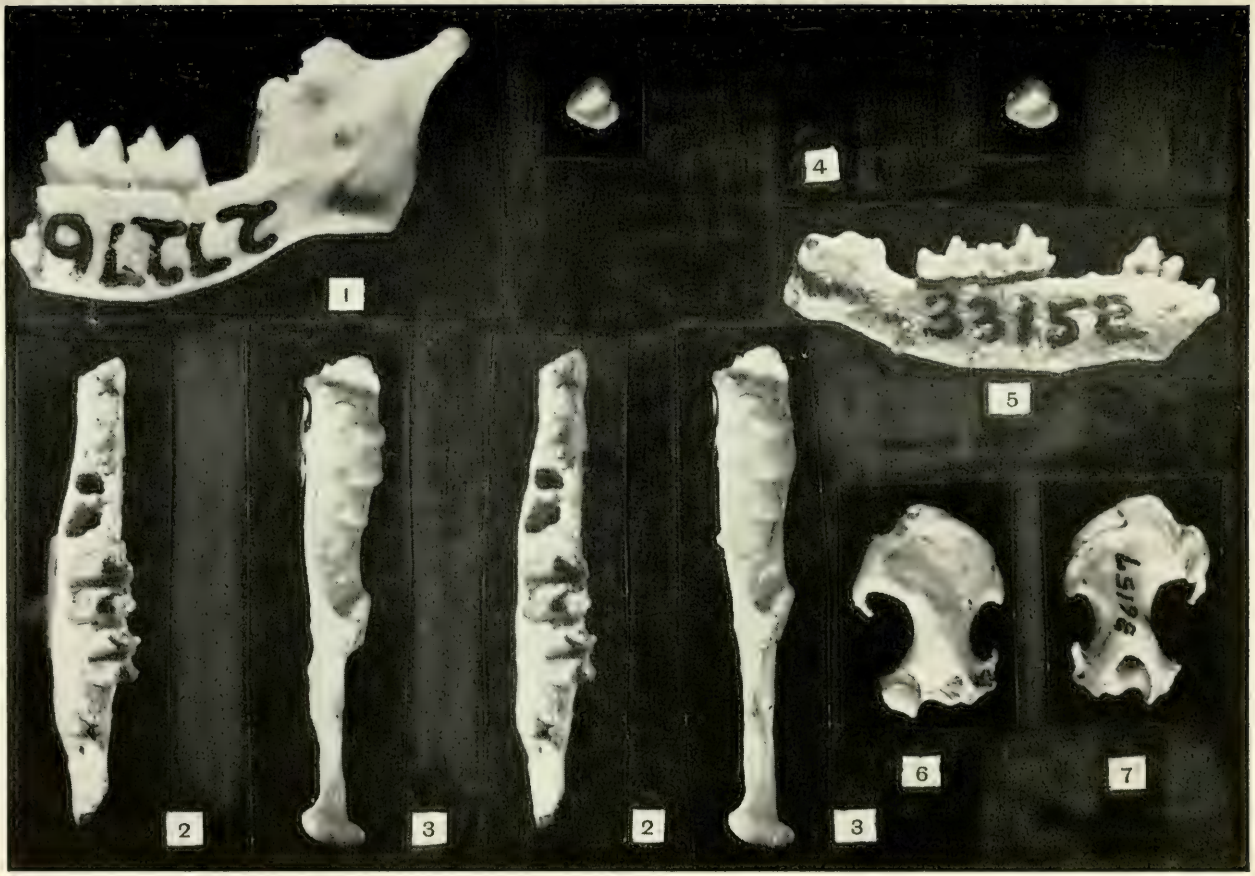
Fig. 3. *Hesperoscalops sewardensis*, UMMP 27276, crown view of right ramus; stereoscopic pair. 3 x.

Fig. 4. *Domninoides valentinensis*, UCMP 36155, P^4 left, crown view; stereoscopic pair. 3.25 x.

Fig. 5. *D. valentinensis*, UCMP 33152, left ramus, lingual view. 3.25 x.

Fig. 6. *D. valentinensis*, UCMP 36157, right humerus, anterior view. 1.75 x.

Fig. 7. *D. valentinensis*, UCMP 36157, right humerus, posterior view. 1.75 x.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BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. OCTOBER 15, 1962 NUMBER 169

NEW RECORDS OF INSHORE FISHES FROM THE ATLANTIC COAST OF PANAMA

BY IRA RUBINOFF[1] AND ROBERTA W. RUBINOFF

During February, March, and April, 1961, a collection of inshore fishes from both coasts of the Isthmus of Panama was made in connection with a study of the effects of geographical isolation on fish speciation. This collection consisted of 2095 specimens of 136 species. A total of 907 specimens of 47 species was taken from the Pacific coast and 1188 specimens of 89 species were collected on the Atlantic coast. Fourteen species in the latter collection were found to represent extensions of known ranges and some of these are sufficiently abundant to be considered resident members of the Panamanian fauna. The purpose of this paper is to report the new records from this area. Notes are also included on three species represented in previous collections from Panama by only one or two specimens each. All the specimens discussed herein are in the collections of the Museum of Comparative Zoology.

Rotenone poisoning of coral pools and lagoons was the principal method of collecting, although occasionally sandy beaches were seined. All of the new records are from coral reef areas, particularly from the reefs bordering the Galeta Point Naval Station near Coco Solo in the Canal Zone.

Most of the smaller eels were collected when the incoming tide overflowed poisoned coral pools onto the exposed surfaces of the reefs and into small crevices and burrows in the coral. When the poison reaches these burrows the inhabitants are driven onto the flat of the reef and are easily collected. Many young specimens of Muraenidae as well as most of the specimens of Moringuidae and Echelidae were collected in this manner.

[1]This research was supported in part by a Public Health Service Training Grant to the Department of Biology at Harvard University, Cambridge, Massachusetts, and in part by a fellowship from the Woods Hole Oceanographic Institution during the summer of 1961.
Contribution No. 1253 of the Woods Hole Oceanographic Institution

In their classic work on the marine fishes of Panama, Meek and Hildebrand (1923, 1925, 1928) collected 236 species from the Atlantic coast, of which only five were eels. In other collections from this area, the apodes are one of the poorest represented groups. Numerous species are known to range along the Atlantic coast north and south of Panama but have yet to be recorded there. Of the nine species of apodes in our collection seven represent new records for this area.

Specimen lengths are standard lengths to the nearest millimeter in all cases except the eels, for which total lengths are given.

The authors wish to thank the following people for making this part of our study possible: Dr. Sydney Galler and Mrs. Helen Hayes of the Biology Branch of the Office of Naval Research, Dr. L. P. Schultz of the United States National Museum, and Dr. Martin Moynihan and Mrs. Adela Gomez of the Canal Zone Biological Area.

Dr. James E. Böhlke of the Philadelphia Academy of Sciences most kindly identified some of the eels.

SPECIES NOT PREVIOUSLY RECORDED FROM THE ATLANTIC COAST OF PANAMA

XENOCONGRIDAE

Kaupichthys atlanticus Böhlke
MCZ 41455-58
Five specimens, 50-205 mm. long, were taken from coral reefs at Galeta Point. These specimens agree with the description of Böhlke (1956).
Range: Tropical western Atlantic from Bermuda to south of Jamaica.

MORINGUIDAE

Aphthalmichthys mayeri (Silvester)
MCZ 41459-61
One specimen, 275 mm. in length, was taken from the edge of a reef southwest of Las Palmas mountain about two-thirds of the distance from Maria Chiquita to Porto Bello. This fish had a distinctly pink head and pink-orange body. This color faded to a dull yellow two days after preservation. Three specimens, 150-330 mm. long, were taken from the exposed surface of Galeta Point Reef.
Range: Bermuda, Florida, Puerto Rico.

ECHELIDAE

Myrophis egmontis Jordan
MCZ 41462-64
Twelve specimens, 81-231 mm. in length, were obtained from Galeta Point. These specimens may be differentiated from Echelidae previously recorded from Panama by the following characteristics: origin of dorsal fin behind the vent, and absence of teeth on the vomer. These eels were found in situations similar to those of *Aphthalmichthys mayeri.*
Range: Florida, Bahamas, West Indies.

MURAENIDAE

Enchelycore nigricans (Bonnaterre)
MCZ 41465-67
Seventeen specimens of this eel, 81-545 mm. in length, were taken from the reefs at Galeta Point.

The slitlike posterior nostril diagnostic of *Enchelycore* is an unreliable character in separating young specimens from other Muraenidae. Separation of the young of *E. nigricans* from *Gymnothorax moringa* which it closely resembles, was facilitated by two characters. The anterior nostrils of *Enchelycore* are shorter than those of *G. moringa* and the upper jaw of *Enchelycore* has a series of 4-6 long canine teeth medial to the outer row of teeth on both sides. All *Gymnothorax moringa* which we examined have 1-3 teeth in this series.
Range: Bermuda, West Indies.

Gymnothorax vicinus (Castelnau)
MCZ 41468,69
Four specimens, 145-330 mm. in length, were taken at the Galeta Point reefs.
Range: Bermuda, West Indies to Brazil, Cape Verde Islands and Africa.

Gymnothorax moringa (Cuvier)
MCZ 41470-73
The collection contains nine specimens, 64-185 mm. in total length, taken from the reefs at Galeta Point.
Range: Atlantic coast of America from Florida to Brazil, Bermuda, Bahamas, West Indies, St. Helena.

Uropterygius Böhlke (n. sp., in manuscript)
MCZ 41475

One specimen 190 mm. long was collected at Galeta Point. Our specimen was identified by Dr. James Böhlke as a species he is currently describing and it will be designated as a paratype.

AULOSTOMIDAE

Aulostomus maculatus Valenciennes
MCZ 41474
One specimen, 185 mm. long, was taken at Galeta Point.
Range: Bermuda, Florida, Gulf of Mexico, Central American coast of Caribbean, Bahamas, West Indies.

HOLOCENTRIDAE

Holocentrus coruscus Poey
MCZ 41476
One specimen, 45 mm. long, from Galeta Point, has the following meristics: D-XI, 12; A-IV, 8; gill rakers 9. Color of fresh specimen: dorsal surface of head red; body red and white lateral stripes; caudal fin red; anal and second dorsal dark red at distal portions; interspinous membranes of dorsal peppermint striped, black spot distally between first three dorsal spines. With the exception of the number of gill rakers this specimen fits the description of *H. coruscus* by Woods (1955) in his revision of the Western Atlantic species of *Holocentrus*.
Range: Bermuda, Florida, Bahamas, West Indies.

APOGONIDAE

Apogonichthys stellatus Cope
MCZ 41477
Two specimens, 12 mm. and 29 mm. in length, were taken from the edge of a reef southwest of Las Palmas mountain about two-thirds of the distance from Maria Chiquita to Porto Bello.
Range: Bermuda, Florida, Bahamas, West Indies.

LABRIDAE

Thalassoma bifasciatum (Bloch)
MCZ 41478-83
Fifty-eight specimens 19-83 mm. in length, were taken at Galeta Point. Although this species has not been previously recorded from Panama it is one of the most abundant representatives of the reef pool fauna. Many more examples were seen than were collected.
Range: Bermuda, Florida, Bahamas, West Indies, Honduras.

CANTHIGASTERIDAE

Canthigaster rostratus (Bloch)
MCZ 41484, 85
We collected eleven specimens, 19-42 mm. in length, at Galeta Point. Ten of these specimens have the fin formula D-10, A-9; one specimen has D-9, A-9. These specimens agree with the description of Breder (1927). Jordan and Evermann (1898), Evermann and Marsh (1900), and Nichols (1930) report specimens with the fin formula D-6, A-8. For a partial explanation of this discrepancy see Breder (1927).
Range: Bermuda, Florida, West Indies, Venezuela and Madeira.

CLINIDAE

Labrisomus kalisherae (Jordan)
MCZ 41486, 87
Six specimens, 25-68 mm. in length, were found in Galeta Point reef pools. One 56 mm. specimen taken in the first week of April possessed enlarged ovaries from which ova 0.5 mm. in diameter were obtained. A 54 mm. male also taken at this locality had enlarged testes.
Range: Florida to Brazil.

Labrisomus nigricinctus Rivero
MCZ 41488
One male specimen 45 mm. long was taken at Galeta Point. It was compared with the holotype, MCZ 34150, and with the description given by Springer (1958).

Springer (1959) reports the range extension of *L. bucciferus* and *L. guppyi* to the Atlantic coast of Panama. *L. nuchipinnis* reported by Meek and Hildebrand (1928) and our specimens of *L. kalisherae* and *L. nigricinctus* bring the total recorded number of Atlantic Panamanian *Labrisomus* species to five.

SPECIES RARELY RECORDED FROM THE ATLANTIC COAST OF PANAMA

With the exception of *Dinematichthys cayorum* these species were not collected by Meek and Hildebrand (1923, 1925, 1928).

BLENNIIDAE

Rupiscartes atlanticus (Cuvier and Valenciennes)
MCZ 41489-91

Eight specimens, 39-74 mm. in length, from the coral reefs at Galeta Point are in the collection. The previous record of this species from Panama was a single specimen taken by Fowler (1916) at Toro Point.
Range: Bermuda, Atlantic and Pacific coasts of tropical America, West Indies.

Salarichthys textalis (Quoy and Gaimard)
MCZ 41492
Three specimens, 24-42 mm. in length, were taken at Galeta Point. One 31 mm. specimen was previously collected at Caledonia Bay, Panama, by Breder (1925).
Range: Bermuda, Florida, West Indies, Brazil.

BROTULIDAE

Dinematichthys cayorum (Evermann and Kendall)
MCZ 41493-96
Twelve specimens of this species (*Ogilbia cayorum* of Meek and Hildebrand), 26-51 mm. in length, were collected at Galeta Point. On April 6 some adults were found to contain well developed embryos which could be seen through the body wall. These were extruded in gelatinous strings when a slight pressure was exerted on the abdomens of the females. They were about 5-7 mm. in length and had small yolk sacs. When placed in a bucket of seawater the embryos were free swimming although apparently premature. Fowler (1916) and Meek and Hildebrand (1928) each found only one example of this species.
Range: Bermuda, Florida, Bahamas.

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BREVIORA

Museum of Comparative Zoology

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THE BRAIN OF THE EMU (DROMAEUS NOVAEHOLLANDIAE, LATH)[1]

I. GROSS ANATOMY OF THE BRAIN AND PINEAL BODY[2]

By

STANLEY COBB
and
TILLY EDINGER

The histology of the cerebral hemisphere of the emu has been extensively studied by Craigie (1935a, 1935b, 1940) and three diagrams of the hemisphere have been published. Drawings of the whole brain have also appeared in the literature (Strong, 1911; Küenzi, 1918), and a photograph was published by Anthony (1928). No description of the whole brain, however, is to be found. Since the emu is, next to the ostrich, our largest living bird, and since it belongs to a taxonomically controversial group, it seems of value to describe the brain and compare it with the brains of other birds. Moreover, the emu is considered, by Pycraft (1900) and many others, to be one of the most primitive of birds. The concept of "primitiveness" will be considered in the discussion at the end of this paper.

MATERIAL

Three specimens of *Dromaeus novachollandiae* were collected by S. J. J. Davies in November 1960 in Western Australia for Professor Ernst Mayr, Director of the Harvard Museum of Comparative Zoology. Two of them were kindly given to us by Professor Mayr for neurological study. The heads had been cut off

[1] This spelling of *Dromaeus* is not the one accepted by some newer checklists, but because *Dromiceius* (an alternative spelling) is the perpetuation of a graphological error (Newton, 1896) and because *Dromaius* is a less proper Latinization, it seems better to use the older form.

[2] From the Museum of Comparative Zoology and the Department of Neurology and Psychiatry, Harvard University, and the Laboratory for Psychiatric Research, Massachusetts General Hospital.

This investigation has been aided by grants from the Foundations Fund for Psychiatry and the National Institute of Neurological Disease and Blindness, grant #03429-02.

and skinned, the eyes had been removed, and the specimens had been fixed in 10 per cent formalin solution in the field. After about two months the heads were packed in moist condition and shipped in cellophane bags to the United States. Here the brains were removed from the skulls after making photographs of various stages of the dissections. The brains were then fixed in fresh neutral formalin solution (10 per cent) for a month. One brain (that of Emu #85) was divided into its component parts for weighing and special histological studies. The other brain (Emu #104) was removed, photographed, fixed for a month in 10 per cent formalin as above, and embedded whole in celloidin for serial sectioning. Both are brains of adult males. The first (#85) appears somewhat larger and weighed 27.7 grams; the second (#104) weighed 25.1 grams.

DESCRIPTION

The position of an avian brain within the skull is determined by many developmental factors. The most obvious are the shape of the bill, the size and position of the eyes, the habitual posture of the bird, and the size and shape of the brain itself. Starck (1955) has given an excellent discussion of these relationships and emphasizes the importance of the size of the eye and the position of the orbit. One way of describing the position of the brain is to measure the angle between the cerebral axis and the axis of the bill (Cobb, 1959). In the emu this angle is about 27° (see Fig. 1), an angle somewhat smaller than that of the gull (*Larus argentatus:* 34°) and the grouse (*Bonasa umbellus:* 36°), but distinctly greater than that of the cormorant (*Phalacrocorax auritus:* 15°) which has the straightest (most extended) type of skull and an exceptionally small brain-bill angle.

Besides showing the relation of the brain to the skull, Figure 1 shows the olfactory bulb and membranous sac of the olfactory nasal chamber; the bulb seems to be in direct contact with the chamber, but closer scrutiny shows that there is a space bridged by the short olfactory nerves. When the light, diploic bone of the bill is removed, the sac which forms the lining of the olfactory chamber is revealed. It is a fairly tough structure containing blood vessels and many nerve fibers. It is crossed anteriorly by a branch of the first division of the trigeminal nerve. The main nerve trunk of this division is seen passing through the orbit, close to the optic nerve and up to a point just below the olfactory bulb.

This is the main sensory nerve from the bill, innervating the skin and vibrissae. Its large size suggests that tactile sense in the bill is acute and important.

On opening the olfactory chamber, the most posterior of the three nasal chambers, a well-developed turbinal mound (superior or olfactory concha) is seen on the lateral wall. It is covered with a soft, yellowish epithelium, which becomes thinner and less yellow as it spreads out over the dorsal and mesial aspects of the chamber. A vertical section through the nasal chambers of the bill at this level (Fig. 3) reveals that the concha is raised to a height of about 5 mm. and is slightly constricted at its base, but is not folded into a spiral like the conchae of some vultures and albatrosses (Bang, 1960). A specimen for microscopic examination was taken from the dorsal surface of the olfactory chamber; it shows cells and cilia typical of olfactory epithelium. About 5 cm. anterior to the olfactory concha there is a large nostril (Fig. 1), which is the external opening of the anterior nasal chamber.

The emu has large eyes and the orbits are spacious. As one sees in Figure 1 the brain lies mostly behind the orbit with the olfactory chambers in the bony structures just in front. The optic nerve enters the chiasm and passes directly to the optic lobe of the opposite side of the midbrain (Fig. 2C). The large fascicles of nerve fibers can be seen as they cross. The optic lobe is a large and conspicuous structure (Figs. 1, 2B and 2C). In the lateral view only about one-fifth of it is covered by the overlying hemisphere. In Figure 2B (in which the parts of the brain are slightly separated) the relation of the optic lobe to hindbrain and forebrain is emphasized. It is clearly a part of the midbrain. In fact, the optic lobes are homologues of the corpora bigemina of reptiles, and of the anterior corpora quadrigemina of mammals. They have taken a ventrolateral position in birds, perhaps because it was easier there to make room for the extraordinary tectal development in this class of vertebrates.

The emu brain when viewed from above (Figs. 1A and 2A) impresses one by its triangular shape, with cerebral hemispheres broad posteriorly and narrow anteriorly. The olfactory bulbs protrude, forming the anterior pole of the hemisphere. On the vertex the two sagittal elevations of hyperstriatum stand out conspicuously and are separated from the lateral parts of the hemispheres by a distinct sulcus, the vallecula (Portmann and Stingelin, 1961).

The cerebellum is larger in comparison to the forebrain than in passerine birds. It has a greater diameter dorsoventrally than laterally (Figs. 1 and 2) although the auricles protrude laterally on each side. These lobes, composed of flocculus and nodule, are the only ones that complicate the simple conformation of the cerebellum, the corpus cerebelli being largely a mid-line organ corresponding to the vermis of mammals. Between the anterior surface of the cerebellum (culmen and declive) and the posterior poles of the cerebral hemispheres there is ample space for the pineal stalk and gland.

The lateral view of the brain (Fig. 2B) shows the relative sizes of the main subdivisions. For this photograph the forebrain, midbrain, and hindbrain were slightly pulled apart. The hemispheres of the forebrain are well developed and extend backwards covering parts of the optic lobe and of the cerebellum. The greatest diameter of the hemisphere is 36 mm. and the greatest diameter of the olfactory bulb is 9 mm., giving a ratio of 4 to 1 or 25 per cent. This places the emu among those birds that have large olfactory bulbs (the Gruiformes, Caprimulgiformes, Procellariiformes, Podicepidiformes, and Apterygiformes). In a list of 47 different species of birds, arranged according to the relative size of the olfactory bulb, the largest at the top, the kiwi would come first and the emu seventh (Cobb, 1960). The anterior end of the hyperstriatum accessorium (sagittal elevation or Wulst) is close to the olfactory bulb, and the posterior end shades off into the neostriatum before reaching the occipital pole of the hemisphere. Thus the emu has a large Wulst that reaches well back towards the occipital pole (Figs. 1 and 2) and well forward to a point close to the olfactory bulb.

A comparison of the external configuration of the brain of the emu with that of other birds shows that it resembles most some herons and ducks. In comparing it with Stingelin's (1958) photographs, it is seen to be strikingly similar to the brain of *Ixobrychus minutus* (see his fig. 21 "Zwergreiher").

Seen from below (Fig. 2C) the conspicuous characteristics of the emu brain are: (1) the large, separated olfactory bulbs, forming the anterior pole; (2) the flatness of the ventral aspects of the lateral parts of the two cerebral hemispheres; and (3) the pair of big optic lobes shaped like flasks with their necks joined in the optic chiasm. The cerebellum is so narrow that it is almost hidden by the medulla oblongata, only the flocculi showing on each side. The roots of the third, seventh, eighth, ninth, and tenth cranial nerves show in this view.

The brain of emu #85 (after formalin fixation) weighed 27.7 grams; his body weight was 34 kg. The brain of emu #104 weighed 25.1 grams (also after formalin fixation); body weight 31 kg. This gives a ratio of brain weight to body weight in emu #85 of 1/1227 and in emu #104 a ratio of 1/1235. Little significance, however, should be given to these ratios because it is known that a living emu may vary 30 to 40 per cent in weight during a year due to conditions of food, climate and water supply. The first brain was separated into 8 pieces, for weighing, as follows:

Olfactory bulb (right)	(injured)
Olfactory bulb (left)	0.12 grams
Cerebral hemisphere (right)	8.85 grams
Cerebral hemisphere (left)	8.8 grams
Optic lobe (right)	7.3 grams
Optic lobe (left)	7.3 grams
Cerebellum	4.6 grams
Brainstem	3.9 grams

The brainstem (defined by Portmann, 1946, and named "Stammrest") is the basal mass of nerve tissue made up of thalamus, midbrain (with optic lobes removed) and hindbrain (with cerebellum removed). Portmann's purpose was to choose as his common denominator that part of the brain which varies least in its size relative to the size of the whole bird. That part is obviously the brainstem. He then compares its size to other parts of the brain and, by dividing the weight or volume of the stem into the coresponding value for another part, he obtains his index. This "index of cerebralization" he finds for an emu to be 4.18, obtained by dividing the weight of the "Stammrest" into the combined weight of the two hemispheres. In our emu #85 this index is 17.6/3.9 = 4.5. According to Portmann's list the figures 4.18 and 4.5 both place the emu far below parrots and ravens, but above loons, grebes, and quail. He believes that this quotient gives an expression of the "level of integration" of the brain for each species.

The Pineal Body

In the dissection of emu #104, a large part of the post-central area of the calvarium was left intact and carefully lifted off the brain. The pineal stalk was thus torn away at its attachment to the diencephalon. It is 10 mm. in length and remained attached

to the pineal body (Fig. 4). The body itself is embedded in the dura and lies in a depression of the cranial roof between the anterior and posterior fossae. The dorsal position of the epiphysis is thus clearly demonstrated; it lies between cerebrum and cerebellum at the level of their dorsal surfaces. The stalk leaves the brain at a point just rostral to where forebrain joins midbrain. The pineal body is round and firm, slightly flattened dorsoventrally. It is yellowish in contrast to the white skull. The fibrous envelope is continuous with dura which has strong bands spreading laterally and anteriorly. Removed from the membranes, the pineal body is roughly triangular, 7 mm. long on each side. With stalk attached, it weighs 0.1 gm. after formalin fixation.

DISCUSSION

The description of the gross anatomy of the brain of the emu brings up five points for discussion: 1) the size of the brain, 2) the question of primitiveness, 3) the general shape of the brain in relation to the base of the skull, 4) the size and position of the Wulst, and 5) the topographic relations of the pineal body.

The size of the brain in relation to body size and "intelligence" has been the subject of much study and many pronouncements. Suffice it to say here that in our opinion the relation of brain weight to body weight (so called cephalization) is a ratio too simple to give information of much significance. Portmann's (1952) pioneer work in describing an index of encephalization is an advance in the right direction. Body weight in birds is too grossly variable to be used in comparison to the much more stable brain weight. Small birds may show rapid and marked change in weight. There is good evidence that some birds may lose from 30 to 50 per cent of their body weight in 24 hours during a migratory flight (Odum et al., 1961; Helms and Drury, 1960). The emu, being flightless, lives in a fairly uniform environment and does not go through the prolonged exertion of migratory flights. Its ratio of brain weight to body weight might, therefore, be relatively stable. Actually, in *Dromaeus novaehollandiae* this ratio is approximately 1/1230 (see p. 5). From the weights given by Crile and Quiring (1940) we deduce that the ratio for an ostrich (*Struthio camelus massaicus*) is 1/2929; for a sparrow (*Passer domesticus*) it is 1/23; and for a hummingbird (*Amazilia tzacatl*) it is 1/24. This does not mean that the hummingbird has a "better" brain than the emu. It merely indicates that the

body controlled by the brain of the hummingbird is just as complex as the body of the emu, though much smaller. The question as to which brain is "better," or more highly evolved, is meaningless unless one asks, "Better for what?" Obviously, the hummingbird's brain is better for flight and the emu's better for running.

Another factor relative to brain size must be considered. It has been pointed out by Sholl (1956) that small brains are in general more closely packed with nerve cell bodies than large brains which have more glial structures between neurons. Man has 10.5 nerve cell bodies per cubic micron; a mouse has 142.5.

In short, the need is to learn what parts of the brain, controlling what organs, are larger or smaller in each family of birds. With more investigation into the quantitative anatomy of the brain, some of these questions may be answered. Fritz (1949) has estimated the volume of four parts of the striatum in four different species of birds; he found significant differences, but no correlation with Portmann's cerebral index.

Many authors have spoken of the emu, and in fact all ratite birds, as primitive, but their concept of primitiveness is not clear. Some seem to call these birds primitive because they are flightless and have no keel on the sternum (Leach, 1923), others because they have a straight type of skull base (Streckschädel) (Marinelli, 1928, p. 156). Stingelin (1958) considers those birds, with a small Wulst which lies neither far forward nor far back, to be the less evolved type. The point would seem to be that one must not apply the term primitive in a general way to the emu (or probably any other bird). One should specify in what respect a given type or family is less evolved ("primitive") and in what respect it is more evolved (specialized). Even then, the gaps in our phylogenetic knowledge do not allow us to say whether the ratite sternum is due to a devolution from carinate ancestors or an evolution from cursorial reptiles. The presence of feathers and the avian type of brain suggest strongly a descent from flying ancestors. In respect to running and adaptation to life in open plains one feels confident in saying that the emu is highly evolved.

Much work has been done on the development of the avian skull. Pertinent to an understanding of the shape of the emu's brain are three recent lines of investigation. Duym (1951) described the bending of the base of the skull in different birds and specified four types — the stretched or extended type of

skull and three degrees of bending. Dullemeijer (1960) has related the shape and size of the principal parts of the brain to the amount of bending of the cerebral axis and has described four classes on this basis: 1) stretched skulls with little bending, 2) bending of 20 degrees, 3) bending of about 70 degrees, 4) bending of about 120 degrees. Starck (1955) has shown the great importance of the size of the eye and orbit in determining the shape of the brain and skull.

In the emu one finds a rather extended type of skull and a very large eye and orbit. Our measurements show that there is an angle of about 27 degrees between cerebral axis and bill axis, and a bending of the cerebral axis of about 13 degrees. Thus the emu falls into class "1" in Dullemeijer's grouping. We agree with him in emphasizing that "the position and shape of the brain parts is influenced by the position of the bill and the position and size of the eye." The development of the bill in birds has been remarkably variable, and with these special developments come variations in the bones of the skull and in the conformation of the brain.

As mentioned on page 4, the general shape of the brain of the emu resembles that of *Ixobrychus* but shape in itself is not very significant phylogenetically or physiologically in comparing birds' brains. One feature, however, may be of interest: the size and position of the Wulst, because this ganglion is conspicuous on the surface of the cerebral hemisphere and because its size in relation to that of the hemisphere appears to vary. Unfortunately, however, there are not enough quantitative data concerning the size of the Wulst in various types of birds to make any statements about its significance.

In the lateral and dorsal views of the emu's brain the Wulst is conspicuous (Figs. 1 and 2). Its anterior end is almost in contact with the olfactory bulb. The posterior end reaches back to within 4 mm. of the occipital pole of the hemisphere. This rounded ridge is long and lies parallel to the interhemispheric fissure — hence, the name used by L. Edinger et al. (1903) "Sagittalwulst," translated as "sagittal elevation" by Portmann and Stingelin (1961). Its position in the emu is like that in the pigeon, a bird whose brain resembles Stingelin's (1958) "Grundtypus." But the Wulst of the emu in relation to the rest of the hemisphere is both longer and broader than that of the pigeon.

Stingelin emphasizes the importance of the position of the Wulst. In his chapter entitled "Comparison and extent of striatal fields" there is a comparative description of the striatal

ganglia in 18 species, with clear diagrams of each. He believes that in the "highly evolved" ("hochevolutiert," p. 38) species there is a tendency to marked frontal enlargement of the hemisphere. This is achieved in two ways. In developmental line A the frontal pole is largely Wulst, the rostral end of which is in contact with the olfactory bulb. In developmental line B the frontal pole is made from the neostriatum and ventral hyperstriatum, the Wulst having receded to a position on the vertex by successive caudal shifts. From these observations Stingelin deduces a morphological rank ("Formwert") in relation to the basic type ("Grundtypus"). In developmental line A, crows and owls are considered the more highly developed groups; in line B, the higher ones are snipe, spoonbill (*Platalea*) and parrot, with a plover considered as "lower" and the lapwing as "middle." This rank order seems to be entirely based on cerebral anatomy. Reference is made neither to fossils nor to other characteristics such as brain axis or anatomy of skull.

As descriptions of the different relationships of one ganglion of the brain to another, the figures and exposition of Stingelin have great value, but taken as indicating evolutionary levels they may be misleading. Until one knows the lines of descent from reptilian and avian ancestors, descriptions of such "Entwicklungsgerichtungen" and levels of evolution with "hoher" and "niederer Formwert" are not justified because evolution is the process of phylogenetic transformation, a phenomenon that cannot be observed except in consecutive phases of an ancestral line.

The "Horizontalmodifikationen" (Stingelin's fig. 32) are certainly of interest as showing differences between the brains of living families of birds, but these modifications are not a basis for conclusions concerning evolutionary ancestry. In short, we doubt if any living bird has a conformation of the brain that we are justified in calling *primitive*. The data for making such a judgment are inadequate. On the other hand, research into the relative size of various parts of the brain, such as Fritz (1949) has done in Portmann's laboratory, may give us important leads as to the degree of cerebral developments. Such investigations would be especially useful if correlated with behavior.

We wish to emphasize the possibility of drawing erroneous conclusions when the anatomy of living forms is used as evidence for describing an evolutionary process, disregarding the evidence from fossils. We welcome the opportunity to point to one feature of the emu brain as a graphic argument against a persistent, but erroneous theory. This feature is the position of the pineal body,

so obvious when one looks at the dorsal surface of the brain. The theory is that absence in birds and mammals of a second epithalamic appendage in the pineal area, the "parietal eye" of reptiles, is due to enlargement of cerebrum and cerebellum in the two descendant classes. That concept supposes that the covering over of the diencephalon and mesencephalon by the cerebrum and cerebellum in Aves and Mammalia obstructed the access of epithalamic appendages to the brain surface. This process is believed to have caused devolution and loss of the predominantly sensory, stalked, second organ in the pineal complex which survives only in lizards and the tuatara, the parietal eye.

Actually, among birds, a pineal organ reaching to the level of the cerebral and cerebellar vaults, attached to the skull roof, is not an exceptional occurrence. This is found in our *Dromaeus* and has been previously reported in brains of other ratites (*Struthio, Rhea, Apteryx*) and, as a button-shaped convexity, on the endocranial cast of the extinct *Dinornis* (Starck, 1955). The difference between these recently and carefully prepared specimens and those figured in the literature is not a real difference, but a matter of preparation.

Küenzi's (1918) diagrammatic figures of the brains of 36 different kinds of birds give the impression that no bird possesses an externally visible pineal organ, as do almost all macroscopic figures of avian brains in the literature, including Strong's (1911) figures which show *Dromaeus*. Küenzi, however, mentions in several places (pp. 28, 52, 89) that the pineal body is too firmly embedded in the meninges to be removed with the brain; he reports (pp. 70-71) that the pineal body in all birds studied occupies a median space between the posterior borders of the hemispheres and the front end of the cerebellum, its distal end reaching approximately to their dorsal level. Our observations on *Bubo, Corvus, Gallus, Columba,* and *Larus* agree with those of Küenzi; all have pineal bodies extending into the dura. A recent study on ten embryonic and three later developmental phases of *Larus* (Wetzig, 1961) also clearly testifies against the theory of mechanical suppression in birds of the second (the stalked) organ in the pineal complex of reptiles. The epiphysis extends to the level of the prospective skull roof in an early transitory phase, and again in the last phases of embryogeny. It is then, and remains in the adult, fitted into the space between cerebrum and cerebellum. It is club shaped, its apex coalesced with the dura in contact with the roof of the skull.

Thus, there is more space available than was assumed. The club shape (with the largest circumference distal) suggests that the form is governed by the space available. While we are well aware that the shape of a predominantly glandular organ (Stammer, 1961) has no great significance, we do wish to draw attention to the shape of the epiphysis of the emu. When, as in our emus, the distal expansion is abrupt, its connection with the corpus diencephali a mere stalk (Fig. 4), the avian pineal body strikingly resembles not the reptilian pineal organ, which is more or less sessile, but the reptilian parapineal vesicle with its nervous and vascular stalk — that is, the parietal eye. Krabbe (1961) observed this similarity in an embryo *Cygnus*. Many species of birds similarly demonstrate that there is no obstruction to the development of a parietal eye.

The reason for the absence of a parietal sense organ in birds is obviously not mechanical suppression; it is to be found in the fossil record, namely in pre-avian phylogeny. The presence of a parietal eye is reflected in a corresponding foramen of the roof of the skull. The fossil record of skulls plainly shows that the organ was first present and then lost in innumerable phyletic lines within the classes Pisces, Amphibia, and Reptilia. Birds are an offshoot of the great reptilian subclass Archosauria. Among the many hundreds of known skulls from its various orders, only two have the parietal foramen. Significantly, both the specimens showing that heritage from Palaeozoic ancestors belong to the earliest forms identifiable as archosaurian, each representing the beginning of a suborder of the order Thecodontia, "stem archosaurs" (*Mesorhinus:* Jaekel, 1910, and *Erythrosuchus:* Huene, 1911). These openings in the parietal bones of Archosauria occurred for the last time at the beginning of the Mesozoic era in the earliest Triassic times. It follows that parietal eyes were lost, not within the evolution of birds, but in remote reptilian ancestors some 80 million years before the first, late Jurassic, appearance of feathered animals, and presumbaly more than 100 million years before the modern type of avian brain was evolved.

In the Mammalia, likewise, both recent and fossil conditions plainly contradict the assumption that possession of a parietal photoreceptor became impossible because of progressive brain evolution. In various groups of mammals now living, much or all of the midbrain is dorsally exposed in a gap between cerebrum and cerebellum. Actually, it has long been known that in some bats, lagomorphs, and rodents the pineal gland extends into the

dura mater at the caudal end of the interhemispheric fissure, and this condition has now been found prevalent in studies of a large material from a great number of genera (Pilleri, 1960). The usual absence of a pineal organ in specimens of the rabbit brain is the result of its having been torn off with the tentorium during preparation. Furthermore, endocranial casts show that in most early Tertiary mammals there was a considerable gap between cerebrum and cerebellum. The parietal foramen was obliterated, i.e. the parietal eye had been lost in a pre-mammalian phase of evolution, in this case, in mammal-like Reptilia shortly before the emergence of the new class.

SUMMARY

A description of the gross anatomy of the brain of *Dromaeus novaehollandiae* is presented on the basis of two specimens from Western Australia. The brain is of the extended type. The olfactory bulbs and sagittal elevations of the forebrain, and the optic lobes of the midbrain are comparatively large. The index of encephalization is 4.5. The brains weighed 27.7 and 25.1 grams, respectively. The pineal body lies in a shallow fossa in the roof of the skull and weighed 0.1 gram. It is pointed out in discussion that there is no good reason for considering this brain to be primitive, and that phylogenetic relationships cannot justifiably be deduced from the anatomy of the brains of living birds.

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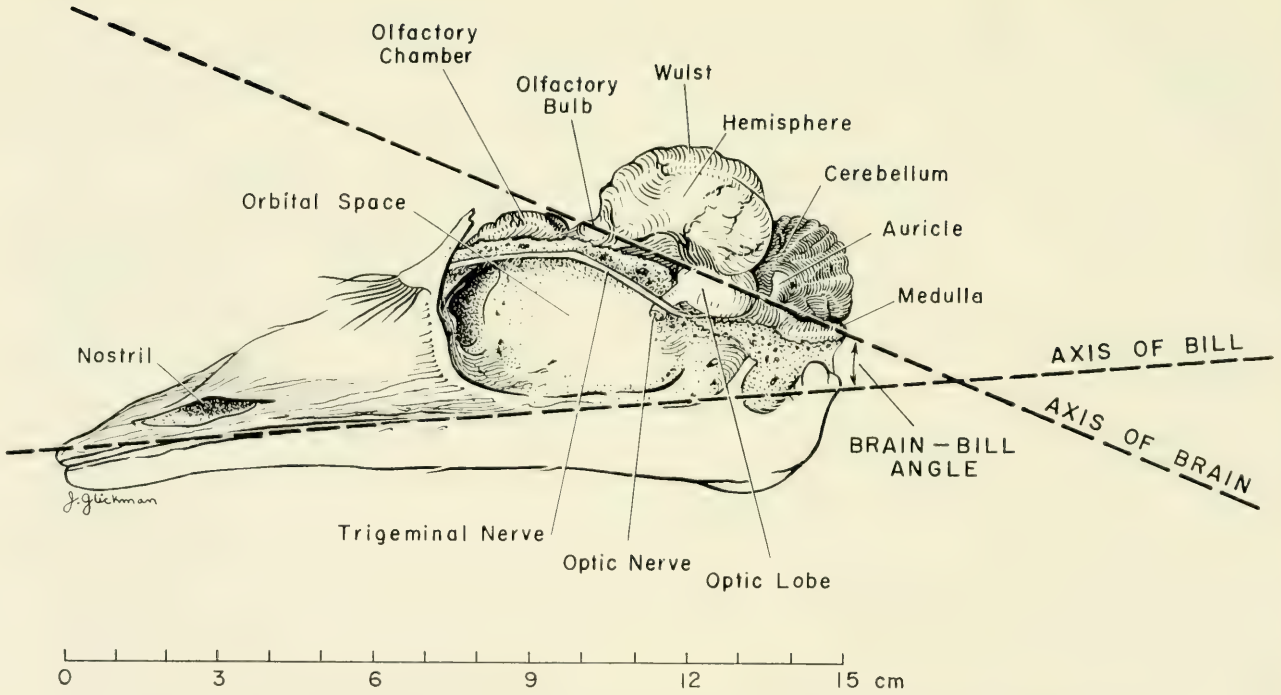

Figure 1A. Drawing of lateral view of brain of emu, in situ on base of skull. Brain-bill angle is 27°.

Figure 1B. Photograph, life size, of dorsal view of same dissection.

FIG 2A DORSAL

FIG 2B LATERAL

FIG 2C VENTRAL

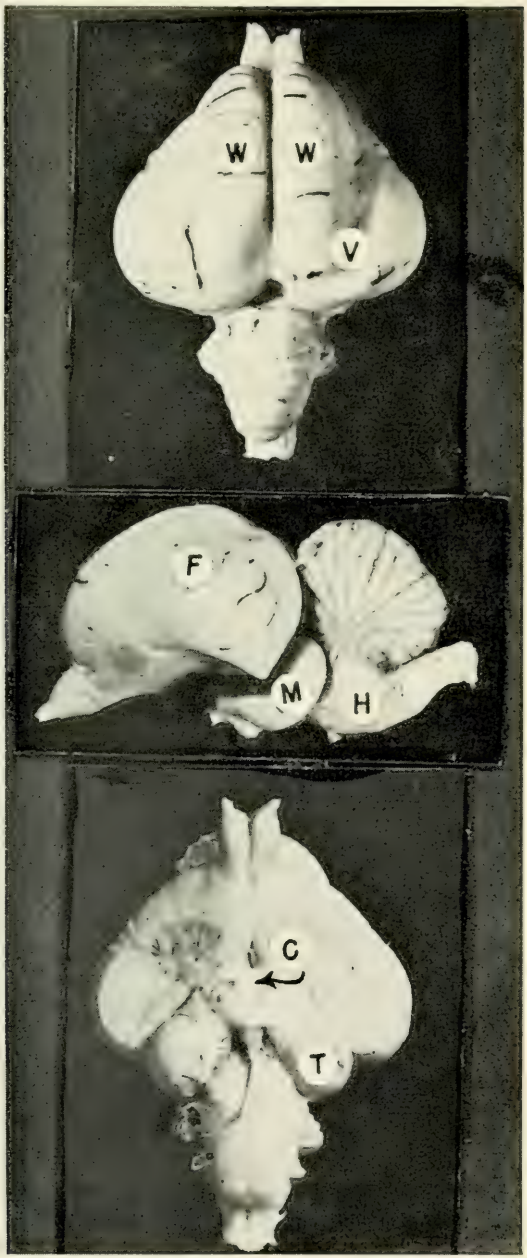

Figure 2. Three views of the brain of the emu (*Dromaeus novaehollandiae*) #104. Life size. *F*, forebrain hemisphere, *H*, hindbrain, *M*, midbrain, showing optic lobe (*T*) and optic chiasm (*C*), *V*, vallecula, *W*, Wulst or hyperstriatum accessorium.

FIG 3

FIG 4A

FIG 4B

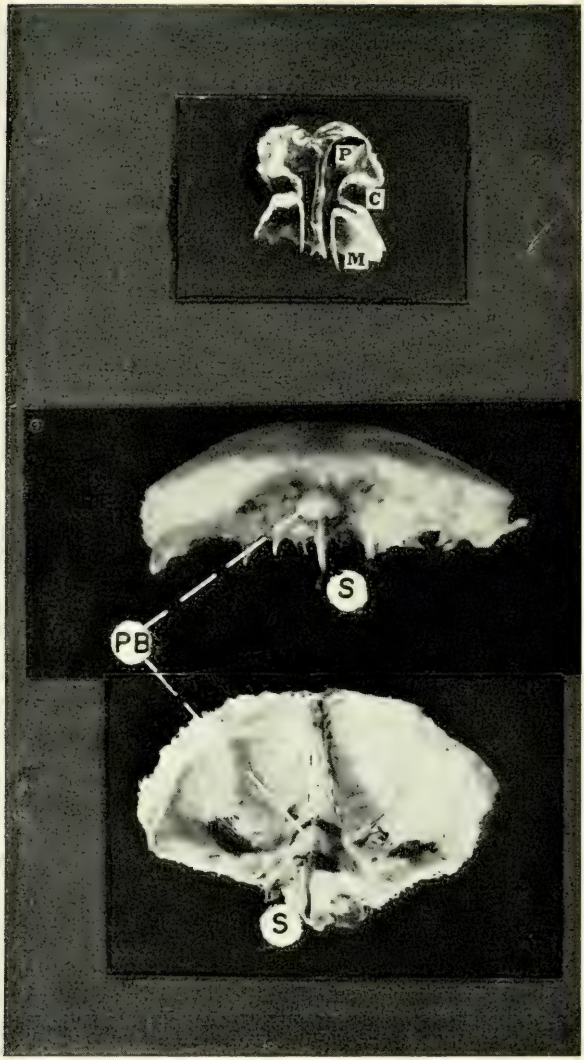

Figure 3. Section through the nasal chambers cut in frontal vertical showing the olfactory (or posterior) chamber (*P*) into which protrudes the olfactory *concha* (*C*) covered with yellow olfactory epithelium. Below is seen part of the middle nasal chamber (*M*). The two chambers are divided by the *septum*. They connect anteriorly with the anterior chamber and the external nostril. Life size.

Figure 4A. Photograph, life size, of pineal body (*PB*) lying in shallow cavity of the calvarium, posteroanterior view. The stalk (*S*) protrudes downward.

Figure 4B. Ventral view, looking upwards at under surface of calvarium. The stalk (*S*) is bent backwards.

BREVIORA

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NOTES ON AMPHISBAENIDS (AMPHISBAENIA; REPTILIA). 6. REDESCRIPTION AND RANGE EXTENSION OF *AMPHISBAENA SPURRELLI* BOULENGER.

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In 1915 Boulenger (p. 659) described the new species of *Amphisbaena spurrelli*, characterized primarily by the presence of tubercular or subconical segments on the dorsal surface of the tail. The two syntypes were collected at "Anda Goya [Colombia], at the junction of the R. Condoto and San Juan." The only subsequent record of the species (Burt and Burt, 1931, p. 40) is the citation of a single specimen (A.M.N.H. 18261) from the neighboring locality of "Boca de la Raspadura," Colombia, without supplementary description.

The present note is based upon a re-examination of these three and of two additional specimens, one of which extends the range of *A. spurrelli* into Panama. The original description has been amended and rewritten according to the standard pattern (Gans and Alexander, 1962). Simple, non-idealized illustrations are included in the present paper.

It is a pleasure to acknowledge the support of the National Science Foundation (NSF G-9054, G-21819). Examination of the types was made possible by assistance from the estate of Leo Leeser. Specimens were examined through courtesy of C. M. Bogert, The American Museum of Natural History (A.M.N.H.), Miss Alice G. C. Grandison, British Museum (Natural History) (B.M.), R. F. Inger and H. Marx, Chicago Natural History Museum (C.N.H.M.), and E. E. Williams, Museum of Comparative Zoology (M.C.Z.). I am particularly grateful to Dr. Federico Medem who made the C.N.H.M. specimen available, and to Miss C. Rhodes for technical assistance.

Amphisbaena spurrelli Boulenger, 1915.

Amphisbaena spurrelli Boulenger, 1915, p. 659. Terra typica: "Anda Goya, at the junction of the R. Condoto and San Juan," Colombia. LECTOTYPE: B.M. 1915.10.21.9 (by present designation). PARATYPE: B.M. 1915.10.21.8.

Diagnosis: A form of *Amphisbaena* without fusions of head scales; with 4 oval [not round] precloacal pores; and with the dorsal and lateral surfaces of the caudal tip covered with conical or tubercular segments. Specimens have 218 to 222 body annuli; 18 to 20 caudal annuli; 16 to 18 dorsal and 16 to 18 ventral segments per midbody annulus; and one row of postgenial and one row of postmalar chin shields. There is no visible autotomy constricton of the tail. Autotomy takes place after the seventh annulus.

Notes on the types: Boulenger (1915, p. 659) illustrated the smaller of his syntypes, which has here been chosen as a lectotype. The types, still extant and in good condition, suggest that his illustrations were idealized, and several of his counts [shown

Fig. 1. *Amphisbaena spurrelli.* Map showing localities mentioned in text. Anda Goya and Boca de la Raspadura are actually closer together than can be indicated on a map drawn to this scale.

in brackets in the table] erroneous. The errors do not affect the validity of the species.

Description: Meristic characters are listed in the table. Figure 3 shows the head scalation, Figure 4 the segmentation of cloaca and tail, Figures 5 to 8 photographs of head, midbody pattern and tail.

Preserved specimens are various [faded] shades of brown dorsally, somewhat lighter ventrally. The darker dorsal color is in part produced by a darkening of the rectangular center of each segment, the contrast with the lighter segmental margins giving the impression of dark spots. The fully dark dorsal spots descend the sides to approximately the third ventral below the lateral groove on each side. Ventrad from this the dark center shrinks drastically or may fade out entirely. The anterior fifth (M.C.Z. 39784), or the head alone, lacks the dark colored segments.

The head scalation shows some variability and no major fusions. An azygous rostral barely visible in dorsal view is followed by three pairs of enlarged cephalic shields in contact along the dorsal midline. The nostrils pierce the first pair (nasals). The second pair (prefrontals) are the largest segments of the head. There are three supra- and two and a half infralabials, as the third infralabial extends considerably beyond the angulus oris. The supralabials are large, the second much the largest. The C.N.H.M. specimen has this segment subdivided differently on both sides. The second infralabials are the largest segments on the lower jaw. Small segments lie beyond the angulus oris in the position of fourth supralabials. The mental is shaped like a truncated wedge with a posteriorly convex tip. The postmental is hexagonal and elongate. It lies in lateral contact with the medial edges of the second infralabials, as well as the anterior portion of the medial edges of the relatively short, wedge-shaped malars. There are one to two rows of postgenial segments, followed by a single postmalar row, the lateral segments of which are slightly enlarged.

The head is relatively blunt, flattened slightly dorsoventrally and oval in cross-section. The lower jaw is but slightly shorter than the upper. The sides of the head would, if extended, intersect some distance anterior to the rostral tip, even in adults

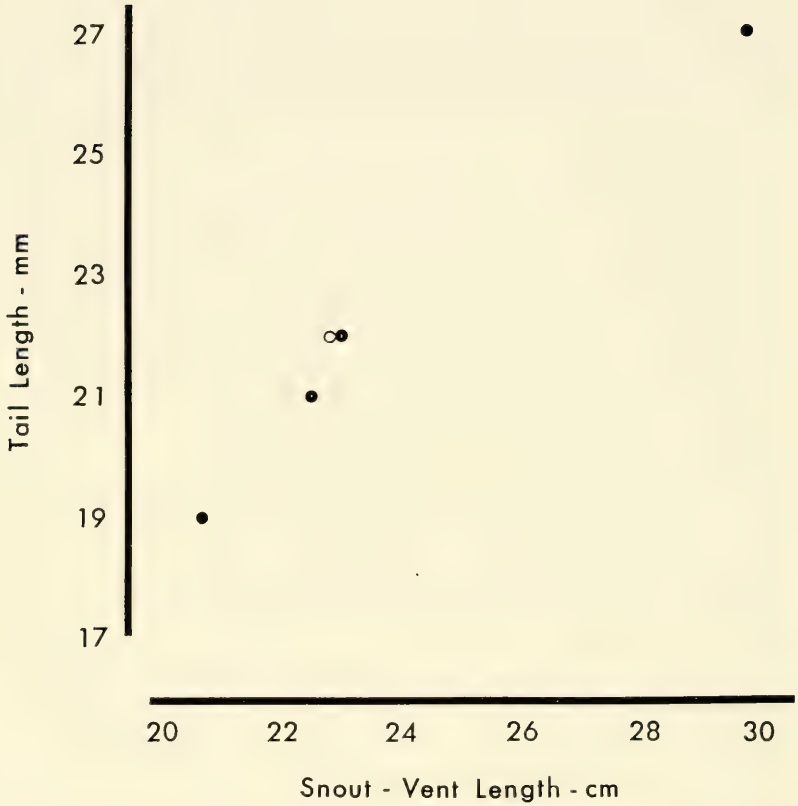

FIG. 2. *Amphisbaena spurrelli*. Scatter diagram showing plot of tail length versus snout-vent length for the available specimens. The lectotype is shown as a hollow circle.

in which the bulge of the temporal musculature changes the outline. The attachment of the skin to the crest of the skull produces a concave dishing of the interfrontal suture, particularly in adult specimens.

The first body annulus curves forward to contact the frontals. Its dorsalmost segments may be somewhat enlarged, and one of the specimens has an intercalated dorsal half-annulus. The second through fifth annuli are narrowed, and the fourth marks the level of the head joint or the point at which the bulge of the temporal musculature returns to normal.

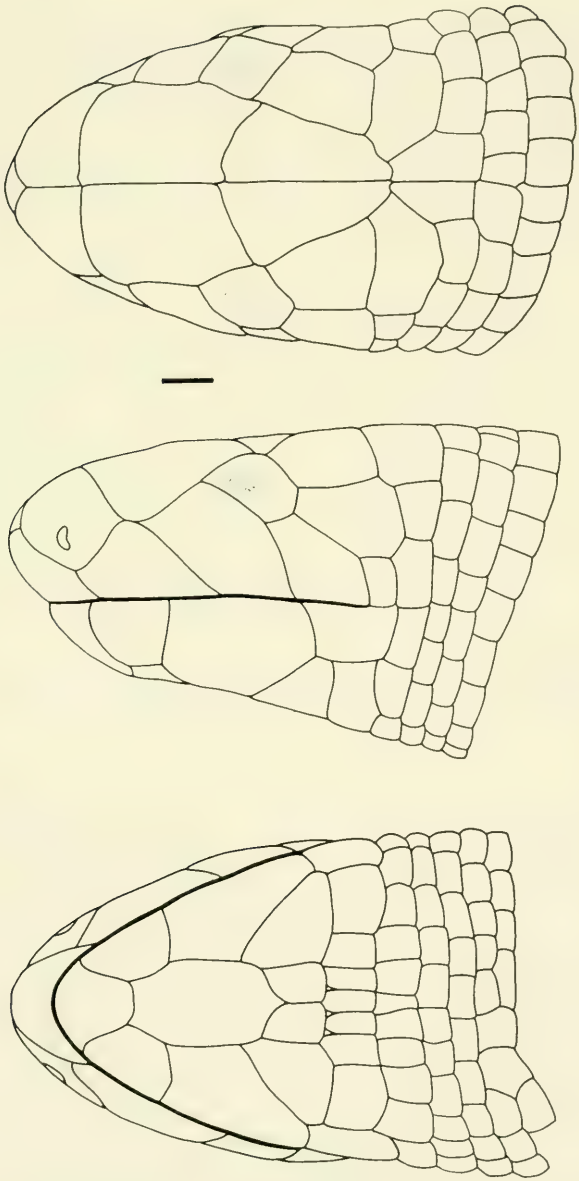

FIG. 3. *Amphisbaena spurrelli.* Dorsal, lateral and ventral views of the head of A.M.N.H. 18261 from Boca de la Raspadura, Colombia. The line equals 1 mm to scale. (V. Cummings, del.).

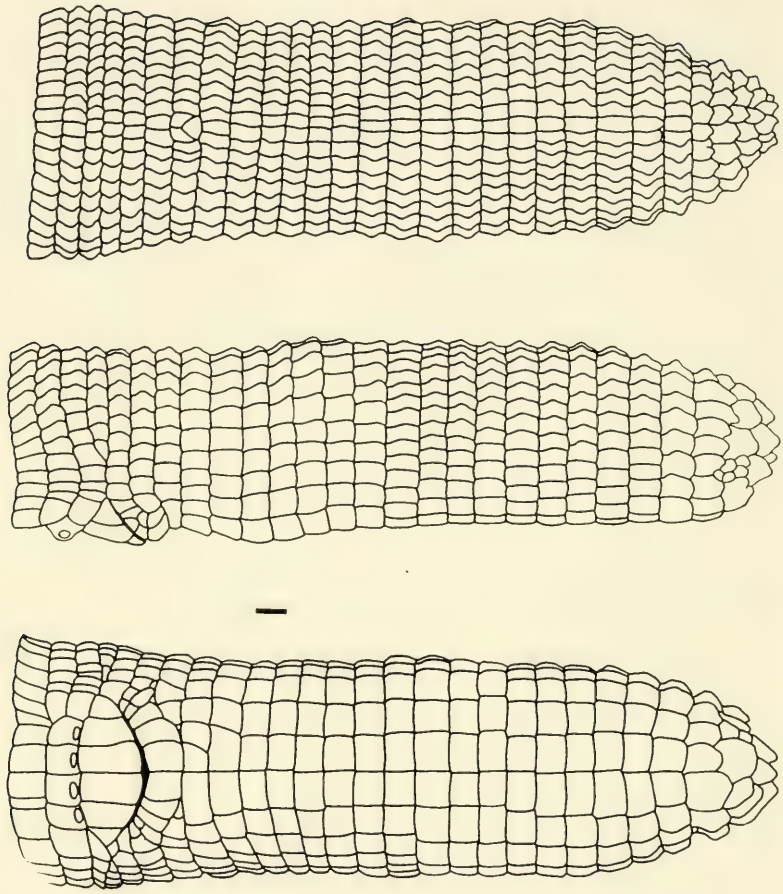

FIG. 4. *Amphisbaena spurrelli*. Dorsal, lateral and ventral views of the cloaca and tail of A.M.N.H. 18261 from Boca de la Raspadura, Colombia. Note the extent of cone formation on the tail and the flattened, slit-shaped precloacal pores. The line equals 1 mm to scale. (V. Cummings, del.).

The dorsal groove is only indicated on the head. The ventral groove is indicated mainly as a gap between aligned segments. The lateral grooves start about one and a half head lengths behind the head joint, and are well defined by a double row of triangular segmental fragments. The middorsal segments are almost twice as long as wide, the midventral segments are almost twice as wide as long.

The oval precloacal pores lie in a single uninterrupted row of normal sized segments anterior to the precloacal shield. The precloacals are characterized by a central group of four somewhat elongate segments. The postcloacals, slightly greater in number, characteristically have a set of two to four midventral and enlarged segments and, flanking these, several split segments entering the cloacal sides. The cloaca may be entirely prolapsed.

The tail becomes gradually wider posterior to the cloacal slit and somewhat higher as well. The ventral surface appears plane and an extension of the precloacal region. The terminal third of the tail shows reduction, with the tip about twice as high as wide. The segments of the dorsal and lateral surfaces are strongly tuberculate or cone-shaped. This character facilitates diagnosis of specimens with intact tails. Caudal autotomy takes place behind the seventh postcloacal annulus (cf. Vanzolini, 1951, p. 23).

Range: Lowland river valleys of northwestern South America, from extreme northern Colombia (Choco) to southern Panama.

Distribution records: COLOMBIA: Choco Province: Anda Goya, mouth of Río Condoto (Boulenger, 1915); B.M. 1915.10.21.8 (PARATYPE), 1915.10.21.9 (LECTOTYPE); C.N.H.M. 130988 [E. R. Dunn? leg. per F. Medem]. Boca de la Raspadura (Burt and Burt, 1931); A.M.N.H. 18261. PANAMA: Tucuti branch, Tuira River [H. C. Clark, leg.] M.C.Z. 39784.

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FIG. 5. *Amphisbaena spurrelli*. Lateral view of the head of the topotype, C.N.H.M. 130988, from Anda Goya, Colombia. Note the irregular subdivision of the second supralabial.

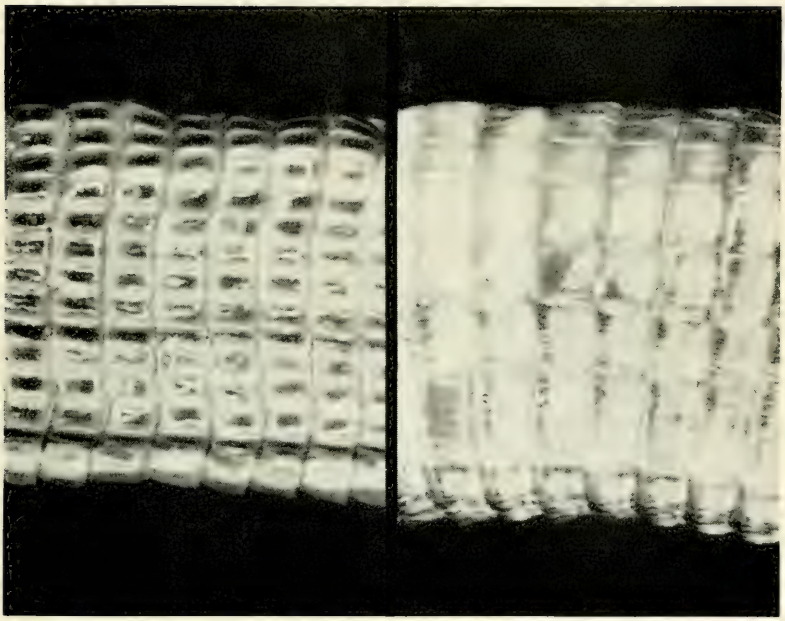

FIG. 6. *Amphisbaena spurrelli.* Dorsal (left) and ventral (right) views of A.M.N.H. specimen at midbody. Note the darkening of the dorsal segmental centers.

FIG. 7. *Amphisbaena spurrelli.* View of caudal tip cross-lighted to emphasize the knobbed nature of the terminal segments.

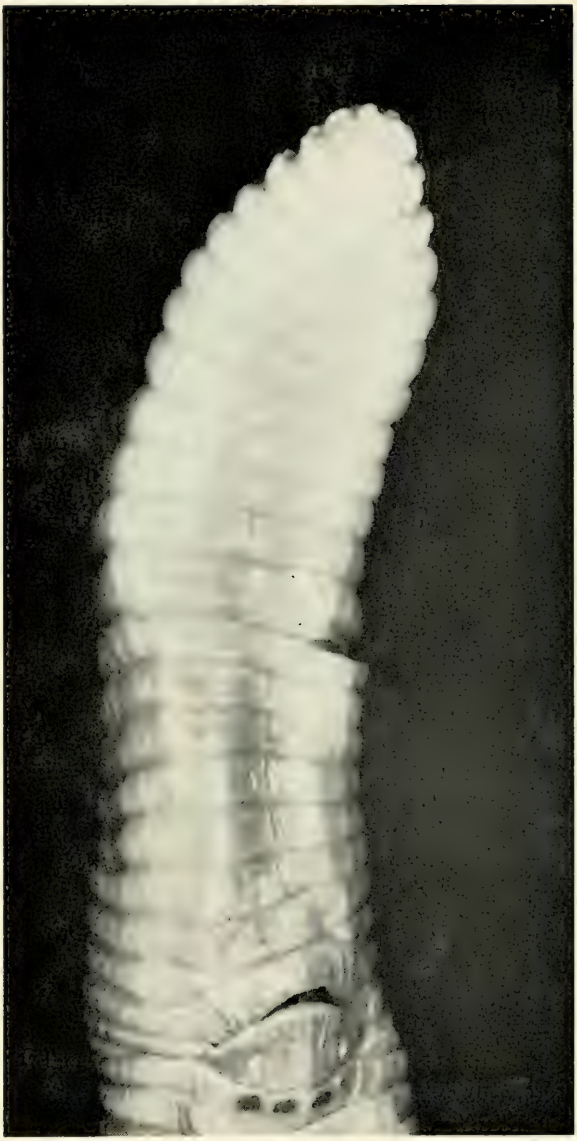

FIG. 8. *Amphisbaena spurrelli*. Ventral view of the cloaca and tail of the A.M.N.H. specimen. Note the onset of autotomy at annulus seven, also the contrast between the plane ventral and conical laterodorsal caudal segments.

Data for five specimens of *Amphisbaena spurrelli*

Collection and number	ANNULI Body	ANNULI Lat.	ANNULI Tail	SEGMENTS Dors./Vent.	SEGMENTS Chin Segm.	SEGMENTS Cloaca	Length
A.M.N.H. 18261	221	4	19	16/17-18	2-7	4-6-12	225+21
B.M. 1915.10.21.8	219	4	19	18/19	3-3-7	4-6	297+27
[Boulenger, 1915]	[213]		[21]	[16/18]			[320+28]
B.M. 1915.10.21.9	218	5	18	16-18/18	2-7	4-6	228+22
[Boulenger, 1915]	[214]		[23]	[18/18]			
C.N.H.M. 130988	222	4/3	19	16/16	(1)-4-8	4-6-13	230+22
M.C.Z. 39784	221	4/5	20	16/18	2-3-7	4-6-12	207+19

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. DECEMBER 14, 1962 NUMBER 172

A NEW SPECIES OF THE RODENT *PIPESTONEOMYS* FROM THE OLIGOCENE OF NEBRASKA

By RAYMOND ALF

Webb School of California, Claremont

In 1956 John C. Donohoe described from the Pipestone Springs formation of Chadronian age in the Montana Oligocene two jaw fragments of a new rodent, *Pipestoncomys bisulcatus*, that he placed in the family Aplodontidae.

The purpose of this paper is to record the occurrence of *Pipestoncomys* in the Chadron formation of Nebraska, to suggest that it be placed tentatively with the castorids rather than with the aplodontids, and to propose a new species of the genus.

North of Crawford, Nebraska, well known exposures of Oligocene sediments occur along the Pine Ridge escarpment. For several years, through the kindness of Frank Arner of Crawford, Nebraska, the Webb School of California has had the privilege of collecting fossils on the Arner ranch. In Sec. 26, T. 33N., R. 53W., Sioux County, Nebraska, are several harvester ant mounds in the Chadron formation, and from these have been collected a rich microfauna including *Pipestoncomys*.

I wish to thank W. D. Turnbull of the Chicago Natural History Museum for the loan of the type specimen of *P. bisulcatus* for study, and Bryan Patterson of Harvard University, and Dr. Mary Dawson of the National Science Foundation for advice. The new species is named in honor of Professor Bryan Patterson. The drawings are by Nick Strekalovsky. The abbreviations refer to the following institutions or collections: C.N.H.M., Chicago Natural History Museum; M.C.Z., Museum of Comparative Zoology; R.A.M., Raymond Alf Museum, Webb School, Claremont, California.

Family CASTORIDAE?

Pipestoneomys pattersoni n. sp.

Type: M.C.Z. no. 7113, fragment of left maxilla with M^{1-2}.

Hypodigm: The type and M.C.Z. nos. 7110, RP^4; 7106, LP^4; 7108, LP^4; 7102, LM^1; 7111, RM^2; 7104, LP_4; 7107, RP_4; 7103, RM_1; 7109, RM_1; 7112, RM_1; 7101, LM_1; and R.A.M. nos. 3072, RM^2; 1683, LM^2; 671, LM^2; 1283, RP_4; 2105, RP_4; 2104, RM_1.

Horizon: The base of the Chadron formation along Pine Ridge is marked by a basal conglomerate resting on the weathered surface of the Pierre shale. The top is characterized by the upper purple-white layer, a continuous purple-tinted white limestone designated by Schultz and Stout (1938) as the boundary between the Chadron and the Brulé formations of the White River group in this area. About half way between this and the basal conglomerate there is a second limestone lens, which is referred to as the lower purple-white layer. The specimens come from well below the lower purple-white layer.

Localtiy: Sec. 26, T. 33N., R. 53W., Sioux County, Nebraska.

Diagnosis: Differing from *P. bisulcatus* as follows: paracone and metacone of M^{1-2} not rounded, paracone and anteroloph not sharply separated, anteroexternal and anterointernal lakes separate, relatively small; M_1 smaller, more rectangular in outline.

Description: The paracone and metacone of M^{1-2}, though distinct and higher than the remainder of the crown, are not the rounded cusps that they are in *P. bisulcatus*. In *P. bisulcatus* the paracone is separated from the anteroloph by a deep groove communicating with the anteroexternal lake, whereas in *P. pattersoni* the separation is very faint. In *P. bisulcatus* the anteroexternal and anterointernal lakes communicate by a slight groove. In *P. pattersoni* the corresponding lakes are completely separate and are also relatively smaller and are more delicately outlined. There is no trace of a mesostyle. P^4 is larger than either M^1 or M^2. A deep groove separates the anteroloph from the rest of the tooth and communicates openly with a deep valley that separates the paracone-metacone loph from the hypocone. On the anteroloph there is a lake below the anterocone and an embayment projecting inward to the protocone. As on the upper molars, a mesostyle is lacking.

The lower first molar of *P. pattersoni* differs in shape from the corresponding tooth in *P. bisulcatus*, being much more rectangular. It is also smaller and more delicate. P_4 is larger than M_1.

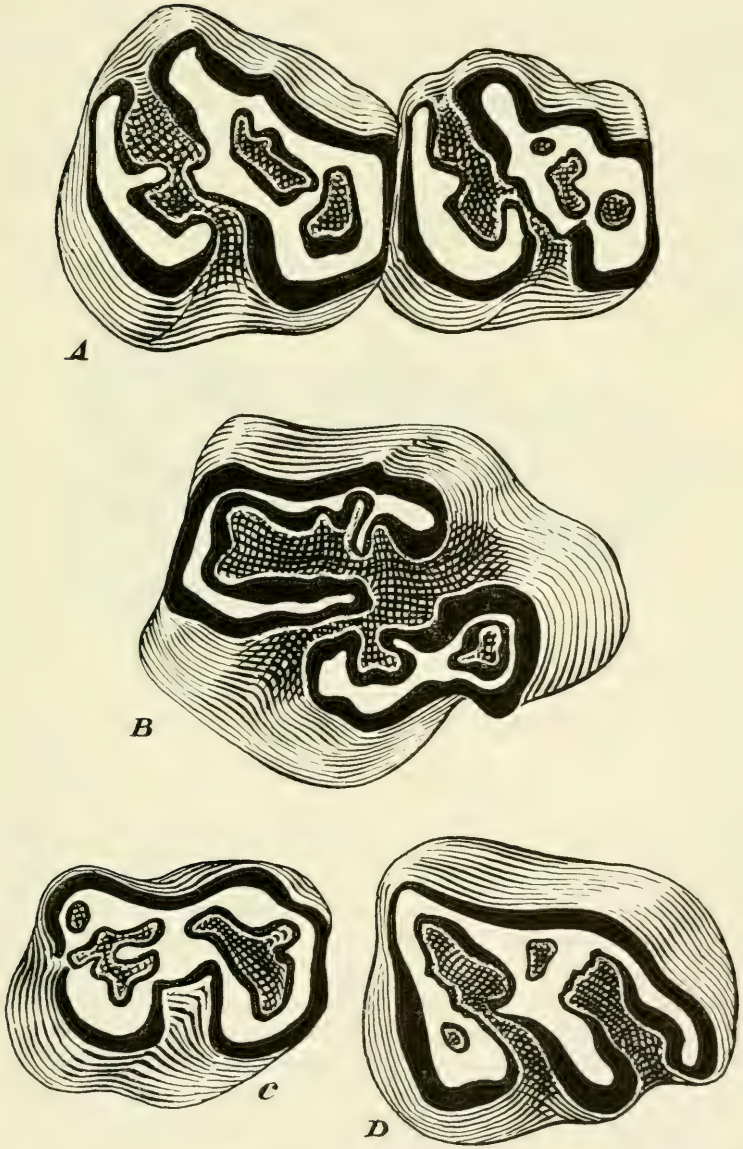

Fig. 1. *Pipestoneomys pattersoni*. *A*, M.C.Z. no. 7113, left maxillary fragment bearing M^{1-2}, type. *B*, M.C.Z. no. 7110, RP^4. *C*, M.C.Z. no. 7103, RM_1. *D*, M.C.Z. no. 7107, RP_4. X 25.

The anterolophid, metalophid, and posterolophid are well developed and separated by deep grooves that terminate at the metaconid and entoconid. There is a lake posterior to the metaconid and one on the posterolophid adjacent to the hypocones.

Discussion: Pipestoneomys, especially in the light of the new evidence reported here, does not fit well into the Aplodontidae. The upper Eocene *Eohaplomys*, the earliest known aplodontid, has the dental formula $\frac{1\ 0\ 2\ 3}{1\ 0\ 1\ 3}$ (Stock, 1935; McGrew, 1941). This formula is retained to the present. The presence or absence of P^3 is indeterminable in the holotype of *P. bisulcatus*, but a

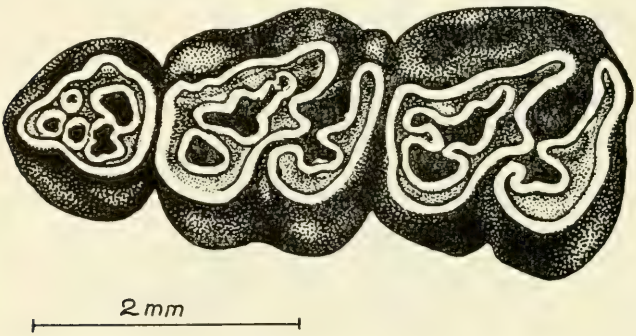

Fig. 2. *Pipestoneomys bisulcatus*. Right M^{1-3}, crown view, C.N.H.M. no. UM 409, type.

small fragment of the maxilla anterointernal to a P^4 of *P. pattersoni* (M.C.Z. no. 7106) shows no sign of the presence of P^3. P_4 are large relative to the molars. The anterior margin of the masseteric fossa in *P. bisulcatus* extends to beneath the middle part of P_4, and the ramus is relatively thick and deep. These characters are not typical of the early aplodontids, but are quite like those occurring in castorids. The cheek tooth structure seems to me to accord better with that of castorids than with that of aplodontids. A lower molar of *P. pattersoni* (M.C.Z. no. 7112) was ground down to show the pattern of a well worn tooth. The median external groove (hypoflexid) persists but its medial portion becomes transformed into a lake, forming a pattern similar in general to that found in, e.g., *Paleocastor* (cf. Fig. 3 and Stirton 1935, Fig. 30). The incisor enamel of Recent *Castor*, Miocene *Paleocastor*, and Oligocene *Agnotocastor* is characterized by an orange

color (Wilson 1949), that of aplodontids is not pigmented. Among the many incisors picked out of the ant mounds are a few with orange color, and those of appropriate size could well belong to *P. pattersoni.*

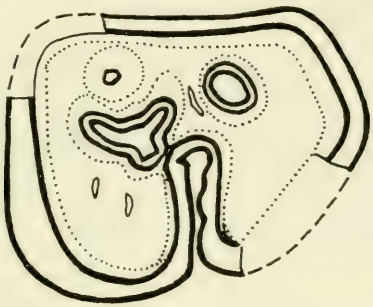

Fig. 3. *Pipestoneomys pattersoni.* M.C.Z. no. 7112, RM_1 ground down to show pattern near base of crown. X 25.

The past and present distribution of aplodontids is also of some interest in this connection. Not only is the range of Recent *Aplodontia* limited to a strip along the west coast of North America, but no unquestioned fossil form has been found east of the Great Basin.[1] If this picture of geographic distribution is adequate, we may have another item of evidence that argues against aplodontid affinities for *Pipestoneomys.*

Pipestoneomys seems to me to fit more reasonably into the Castoridae than into the Aplodontidae, and I know of no other family of appropriate range to which it might be referred. If this tentative assignment is correct, the genus is the earliest beaver so far known, although its position in castorid phylogeny is uncertain.

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[1] Shotwell, in his interesting study of the aplodontids (1958), mentions *Pipestoneomys* only in passing, noting that *P. bisulcatus* occurred well to the east of the other known fossils.

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TABLE 1

Pipestoneomys. Upper Dentition

Measurements in millimeters

	P. pattersoni		*P. bisulcatus* C.N.H.M. UM 409, type
Crown length			
M^1	M.C.Z. 7102	1.62	1.78
	M.C.Z. 7113	1.47	
M^2	M.C.Z. 7111	1.48	1.6
	M.C.Z. 7113	1.23	
	R.A.M. 671	1.48	
	R.A.M. 1683	1.62	
	R.A.M. 3072	1.44	
P^4	M.C.Z. 7106	2.16	
	M.C.Z. 7108	2.07	
	M.C.Z. 7110	1.98	
Greatest width			
M^1	M.C.Z. 7102	1.71	1.95
	M.C.Z. 7113	1.67	
M^2	R.A.M. 1683	1.62	1.81
	R.A.M. 671	1.44	
	M.C.Z. 7111	1.35	
	M.C.Z. 7113	1.67	
	R.A.M. 3072	1.35	
P^4	M.C.Z. 7106	1.98	
	M.C.Z. 7108	2.09	
	M.C.Z. 7110	1.94	

TABLE 2

Pipestoneomys. Lower Dentition

Measurements in millimeters

	P. pattersoni		*P. bisulcatus* C.N.H.M. UM 408
Crown length			
M_1	M.C.Z. 7101	1.44	1.83
	M.C.Z. 7103	1.48	
	M.C.Z. 7109	1.74	
	M.C.Z. 7112	1.89	
	R.A.M. 2104	1.62	
P_4	M.C.Z. 7104	1.62	dP_4 1.78
	M.C.Z. 7107	1.51	
	R.A.M. 1283	1.80	
	R.A.M. 2105	1.71	
Greatest width			
M_1	M.C.Z. 7101	1.51	1.69
	M.C.Z. 7109	1.62	
	M.C.Z. 7112	1.62	
	M.C.Z. 7103	1.35	
	R.A.M. 2104	1.53	
P_4	M.C.Z. 7104	1.35	dP_4 1.18
	M.C.Z. 7107	1.42	
	R.A.M. 1283	1.48	
	R.A.M. 2105	1.62	

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. DECEMBER 24, 1962 NUMBER 173

NEW SPECIES OF LAND MOLLUSKS FROM THE REPÚBLICA DOMINICANA

By

WILLIAM J. CLENCH

We are deeply indebted to Drs. Stanley Rand, Clayton Ray and Juan Rivero for two important collections of land mollusks collected in the República Dominicana. Both collections were made in areas hitherto unknown as far as the land mollusks were concerned. Of the four species herein described, two represent a subfamily and a genus not previously known from Hispaniola. Probably one-third of the species are known only from their type localities, the remaining two-thirds from a very few localities. For this reason it is impossible to give significant distributional patterns of any one species, and but few generic patterns. Our present knowledge of the land and freshwater mollusks of Hispaniola is probably only about ten percent, compared with that of Cuba. Much of this is due, of course, to the fact that there are no local interested persons in Hispaniola. Cuba has had a host of highly trained naturalists, such as Juan Gundlach, Charles Wright, Filip Poey, Rafael Arango, Carlos de la Torre, P. J. Bermudez and C. G. Aguayo. All have made extensive collecting trips throughout most of Cuba and their interest stimulated many others to collect. As a consequence, there are comparatively few areas in Cuba where the fauna still remains unknown. Conversely, Hispaniola has had none of the local stimulation, and what is known of the area has been gathered by outsiders on a few expeditions such as those made by Auguste Sallé in 1847-1851, D. F. Weinland in 1857, Justus Hjalmarson in 1858, Paul Bartsch in 1917, 1920, and 1929, W. J. Eyerdam in 1927, C. R. Orcutt in 1929-1930, D. C. Pease in 1932 and W. J. Clench, R. A. McLean and H. D. Russell in 1937. Many others have contributed material, much of it secondary to other zoological or botanical pursuits (see Crosse 1891, and Bartsch

1946). There remains much territory on this island about which nothing is known, particularly the central mountain system, the Cordillera Central.

HELICINIDAE

Helicina juliae, new species

Plate 1, figure 2

Description. Shell reaching 8 mm. in greater diameter, imperforate, subglobose, smooth and shining. Color a bright pea-green to yellow with the first 1½ post-nuclear whorls with a broad band of brownish purple, as well as a peripheral band of the same color. Columellar area white and occasionally margined with blue. There may be one or more axial bands which occur only from the peripheral band to the suture above. Whorls 4 and convex. Spire depressed and obtuse. Aperture subtriangular in shape. Outer lip reflected, white, and with a moderate depression behind. Parietal area thinly glazed. Columella very short. Sculpture consisting of very fine growth lines.

Height	Width	
5.5 mm.	8.0 mm.	Holotype
5.1 mm.	7.0 mm.	Paratype

Types. The holotype is in the Museum of Comparative Zoology, no. 168267, from Colonia Ramfis, 20 km. W of San Cristobal, República Dominicana. Dr. Juan Rivero collector, March 1957. Paratypes from the same locality in the Museum of Comparative Zoology and the Academy of Natural Sciences of Philadelphia.

Remarks. This species differs from *Helicina viridis* Lamarck to which it is probably related, by being much smaller and by having several color phases in addition to the axial brown line or lines which extend from the peripheral band to the suture above. *H. viridis* reaches 14 mm. in width and 9.5 mm. in height and is a pure pea-green in color. The two species are the same in shell outline.

Proserpina marcanoi, new species

Plate 1, figure 3

Description. Shell reaching 4.7 mm. in width, depressed, imperforate, smooth and shining. Color a light whitish green. Whorls 5 and convex. Spire depressed. Aperture semicircular.

Outer lip simple. Parietal wall glazed and supporting a high and thin lamella. Columella short and supporting a second lamella which is about one-third as high as the parietal lamella. Umbilical area slightly depressed. Suture defined but not impressed. Sculpture consisting of exceedingly fine growth lines.

Height	Width	
2.4 mm.	4.7 mm.	Holotype
2.2 mm.	4.4 mm.	Paratype
2.1 mm.	4.3 mm.	"

Types. The holotype is in the Museum of Comparative Zoology, no. 188911, from Colonia Ramfis, 20 km. W of San Cristobal, República Dommicana. Two paratypes are in the Museum of Comparative Zoology from the same locality. Dr. Juan Rivero collector, March 1957.

Remarks. This is the first species of the Proserpininae to be recorded from Hispaniola. The subfamily has been known elsewhere only from Jamaica and Cuba. In relationship, it appears to be nearest to *P. depressa* d'Orbigny, a species which is widely distributed in Cuba. It differs from *depressa* by being smaller in size, proportionally higher, and in having a columellar lamella nearly twice as high as the Cuban species.

This species is named for Eugenio Marcano of the Instituto de Investigaciones Botanicas y Zoologicas de la Universidad de Santo Domingo, who collected with Dr. Juan Rivero when he was at Colonia Ramfis in March 1957.

TRUNCATELLIDAE

Geomelania (Merrilliana) riveroi, new species

Plate 1, figure 4

Description. Shell reaching 7.6 mm. in height (truncated), extended, imperforate and strongly sculptured. Color a dull white. Whorls 8 and moderately convex. Aperture holostomatous and attached to the body whorl. Parietal and palatal lips reflected. Columella short and slightly oblique. Suture impressed. Sculpture consisting of numerous axial costae with exceedingly fine spiral threads between the costae. Operculum unknown.

Height	Width	
7.6 mm.	2.0 mm.	Holotype

Types. The holotype is in the Museum of Comparative Zoology, no. 230505, from Colonia Ramfis, 20 km. W of San Cristobal, República Dominicana, collected by Dr. Juan Rivero in March 1957.

Remarks. This is the second known species of *Geomelania* from Hispaniola. It differs from *Geomelania haitiensis* Weinland in being twice as large and in having the axial sculpture coarser and by having 8 whorls, *G. haitiensis* having only 5. In relationship, it appears nearest to *Geomelania elongata* Pfeiffer from Oriente, Cuba, and differs from it by being a little larger, having one more whorl and in being a little more coarsely sculptured.

SAGDIDAE

Zaphysema randi, new species

Plate 1, figure 1

Description. Shell large, reaching 67 mm. in height, smooth, rather thin and globose. Color probably a yellowish brown. Whorls 4½ and strongly convex. Outer lip simple, parietal wall with a thin glaze. Suture slightly indented. Columella long, sinuous and somewhat oblique. Sculpture consisting of very fine axial growth lines.

Height	Width	
65.0 mm.	67.0 mm.	Holotype
67.0 mm.	67.5 mm.	Paratype

Types. The holotype is in the Museum of Comparative Zoology, no. 230503, from Cueva de San Francisco, Cerros de San Francisco, Mun. Pedro Santana, San Rafael, República Dominicana. Collected by Stanley Rand and Clayton Ray, August 1958. There is single paratype from the same locality.

Remarks. This species is placed provisionally in the genus *Zaphysema*, a genus heretofore known only from Jamaica and Navassa islands. It is about three times as large as the largest Jamaican species, *Zaphysema macmurrayi* C. B. Adams. Both specimens were dead when found in the cave and appear to be quite old as they are white and completely devoid of periostracum.

This species is as large as the largest *Polydontes gigantea* Scapoli from Hispaniola and *Zachrysia petitiana* d'Orbigny from the Trinidad Mountains of Cuba. Its large size and thinner shell makes it more capacious than either of these two species.

This is by far the largest species in the family Sagdidae, a family which occurs in the West Indies, southern United States,[1] and south through Central America and northern South America. Its greatest generic development is centered in the island of Jamaica.

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[1] A single genus, *Microphysula*, with two species, *ingersolli* Bland and *cookei* Pilsbry extends north through the Rocky Mountain states to southern British Columbia.

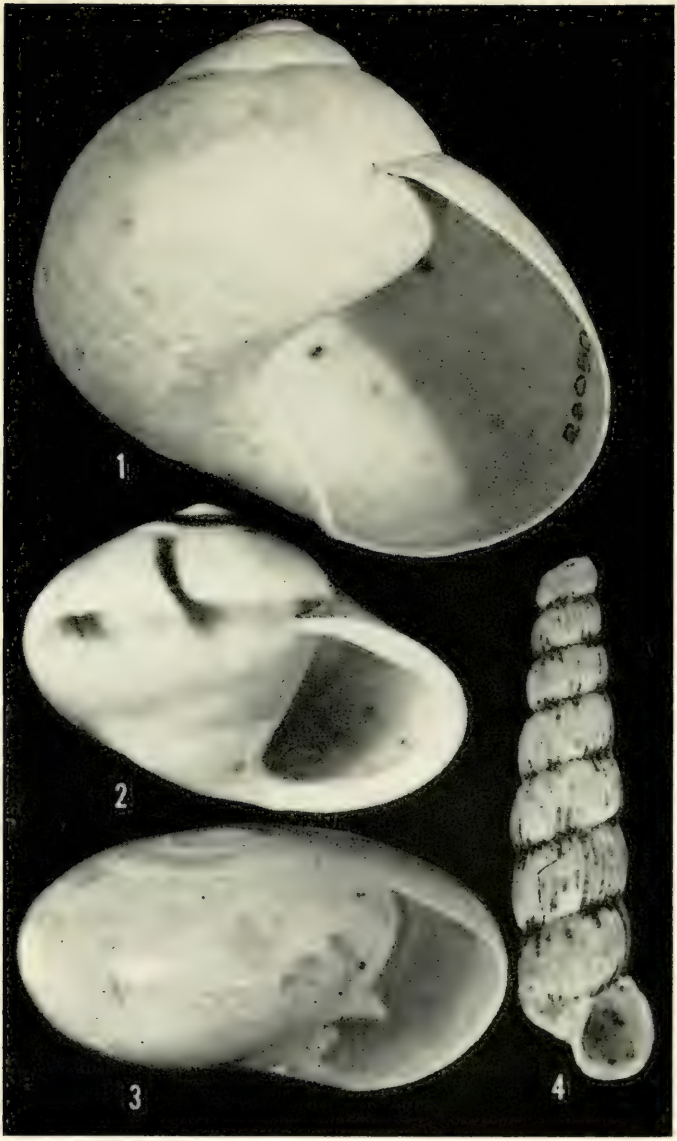
PLATE

Fig. 1. *Zaphysema randi* Clench. Cueva de San Francisco, Mun. Pedro Santana, República Dominicana (about natural size).

Fig. 2. *Helicina juliae* Clench. Colonia Ramfis, 20 km. W of San Cristobal, República Dominicana (7.4X)

Fig. 3. *Proserpina marcanoi* Clench. Colonia Ramfis, 20 km. W of San Cristobal, República Dominicana (13.8X).

Fig. 4. *Geomelania* (*Merrilliana*) *riveroi* Clench. Colonia Ramfis, 20 km. W of San Cristobal, República Dominicana (about 9X).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BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. DECEMBER 24, 1962 NUMBER 174

A NEW ARCTOCYONID FROM THE PALEOCENE OF WYOMING

By Bryan Patterson and Paul O. McGrew [1]

Since 1959, the Department of Geology of the University of Wyoming and the Museum of Comparative Zoology, Harvard University, have been carrying on a joint program of field and laboratory work in the later Mesozoic and earlier Cenozoic vertebrate-bearing formations of Wyoming, paying special attention to those deposits amenable to washing techniques. Much of the work accomplished thus far has been done in the Shotgun member (Keefer, 1961) of the Fort Union formation in the northern part of the Wind River Basin.

Within this member is a bone bed, some twelve to twenty-four inches in thickness, that is extraordinarily rich in vertebrate remains, mostly single teeth of mammals, crocodiles and small sharks. The bed occurs at the base of a sandstone (unit 20 of Keefer's section at Twin Buttes) 217 feet above the base of the Shotgun member, which is 1265 feet in thickness at this locality. Keefer has shown that overlying the lower Fort Union in this region are two essentially contemporaneous, interfingering rock units, the lacustrine (or marine?) Waltman shale and the marginal Shotgun member. The mammalian fauna from the bone bed in the Shotgun is a rich one. From Keefer's sample collection, Gazin (*in* Keefer, 1961) has recorded: *Ptilodus*, *Mimetodon*, *Ectypodus*, *Anconodon*, *Eucosmodon?*, *Catopsalis*, *Peradectes?*, *Gelastops*, *Diacodon?*, possibly *Aphronorus*, *Pentacodon*, possibly *Zanycteris*, cf. *Pronothodectes*, *Claenodon*, *Tricentes*, *Periptychus*, *Anisonchus*, *Promioclaenus*, *Litomylus?*, *Gidleyina* and *Pantolambda*. Our extensive collections will add a number of forms as the work of identification proceeds. The Shotgun member at Twin Buttes has yielded very little in the way of vertebrate material outside of the bone bed.[2] Thus far we have found only a

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[2] During the 1961 season a concentration similar to but less rich than that of the bone bed was found some 90 feet lower in the member.

few fragments of a medium-sized pantodont. We propose that the assemblage be known as the Shotgun local fauna, from the name of the member in which it occurs. The age, so far as can be determined at present, appears to be early Tiffanian. At Shotgun Butte, the type locality, where the member has a thickness of 2,830 feet (Keefer, 1961), *Phenacodus* sp. and *Plesiadapis* sp. cf. *P. cookei*, have been found in the upper part of the sequence (Keefer and Troyer, 1956).

We are greatly obliged to Dr. William R. Keefer for his help in the field. For the opportunity to examine comparative material we are indebted to Dr. C. Lewis Gazin, U. S. National Museum, Dr. Malcolm C. McKenna, The American Museum of Natural History, and Dr. Craig C. Black, Carnegie Museum. During the field season of 1960 we were assisted by James A. Jensen, Lee A. Wooderson, John Zamecnik, Floyd Andrews, Clyde T. Williams, Richard P. Timmermeyer, Charles P. Lyman, Jr., and Robert F. Wallin. The photographs are the work of Miss Linda Loring. The following abbreviations are used: A.M.N.H., American Museum of Natural History; M.C.Z., Museum of Comparative Zoology; U.W., University of Wyoming.

ARCTOCYONIDAE [1] Murray

OXYCLAENINAE Matthew

COLPOCLAENUS [2] gen. nov.

Type species: C. keeferi sp. nov.

Known distribution: Paleocene, early Tiffanian, Wyoming.

Diagnosis: Enamel of molars strongly wrinkled, all crests crenulated, accessory cuspules numerous. Principal cusps of upper M high, massive, tightly grouped; central basin small; protocone nearly central in position with long lingual slope; conules large, blunt, separated by grooves from principal cusps; hypocone small on M^{1-2}, rudimentary on M^3; cingula strong, not continuous around protocones; external cingulum interrupted by labial continuation of sharp cleft between paracone and metacone; upper M wide relative to length. Trigonids of lower M high, short; paraconid internal in position, closely appressed to metaconid, paraconid crest well developed; posterior crest connecting protoconid

[1] One of us (B.P.) proposes to transfer the Arctocyonidae from the Creodonta to the Condylarthra. This transfer and the various questions that it raises will be discussed in a later paper.

[2] Kolpos, a fold and *claenus;* in allusion to the wrinkled enamel of the molars and, in particular, to the curiously folded trigonids.

and metaconid present; protoconids and metaconids with short, centrally situated crests running lingually and labially, respectively, forming a third, transverse trigonid crest; deepest portion of talonid basin near lingual side; hypoconulid of M_3 long, broad, high, cuspidate.

Colpoclaenus keeferi[1] sp. nov.

Type: M.C.Z. no. 8355, LM_3.

Hypodigm: Type and U.W. nos. 1931, LM_3; 1932, RM_3; 1933, LM^1; 1934, RM^3; 1935, LM_2; M.C.Z. nos. 8356, RM_3 (much worn); 8357, LM^2; 8358, RM_2.

Horizon and locality: Shotgun local fauna, Shotgun member of the Fort Union formation; NE¼ SE½, sec. 31, T. 6 N., R. 3 E., ¾ mile SW of the more northerly of the Twin Buttes, Fremont County, Wyoming.

Diagnosis: Sole known species of the genus diagnosed above.

DESCRIPTION

Colpoclaenus keeferi is notable for the massive, high, principal cusps of the upper molars, the elevated trigonids and the extremely rugose enamel. The latter feature disappears after very little wear, as is demonstrated by a moderately worn M_2 (M.C.Z. no. 8358). There can be, we believe, no doubt that the various lower molars represent the same species, and their association with the uppers would appear to be demonstrated by excellent occlusion between M.C.Z. no. 8357, LM^2, and U.W. no. 1935, LM_2, as well as by the general structure.

The upper molars are considerably wider than long, M^{1-2} being essentially quadrangular, M^3 suboval in outline. The protocone is the largest of the three principal cusps; its apex is a little lingual to the center of each tooth of the series, and its lingual face is very long and gently sloping, rather shorter in M^3 than in M^{1-2}. The paracone is more labial in position than the metacone and is slightly larger and higher, being approximately the same height as the protocone. Paracone and metacone are grooved on their basinward faces and are separated by a well marked cleft. The large blunt proto- and metaconules are separated from the primary cusps by grooves and are united by crests to the anterior and posterior cingulum respectively; the protoconule is smaller

[1] For Dr. W. R. Keefer who discovered the Shotgun bone bed in the course of his work on the Fort Union of the Wind River Basin.

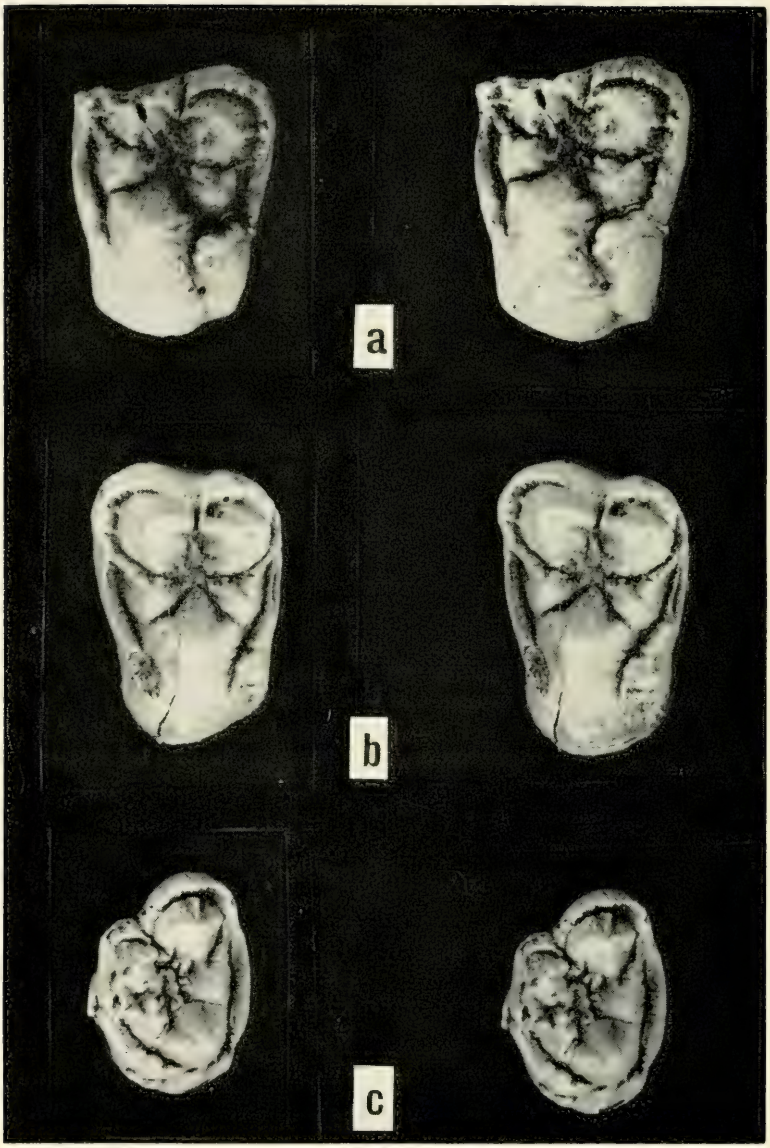

Figure 1. *Colpoclaenus keeferi* gen. et. sp. nov. Upper molars: *a*, LM^2, M.C.Z. no. 8357; *b*, LM^1, U.W. no. 1933; *c*, RM^3, U.W. no. 1934. X3. Stereoscopic views.

than the metaconule on M^{1-2}, about equal to it in size on M^3. The rather shallow basin enclosed by these cusps and conules is situated in the labial half of the tooth and bears various poorly defined cuspules on its floor. A hypocone is differentiated on M^{1-2}, on which it is considerably smaller than the conules, but is barely distinguishable on M^3. Apart from an interruption on the external face, where the cleft between paracone and metacone continues on to the labial margin, a strong, crenulated cingulum runs from the hypocone around the tooth to the antero-internal corner, at which point the cingulum is broken in M^1. M^2 shows no protostylar enlargement here and M^3 a very slight one. With the exception of a slight rise in the cingulum at the parastylar site on M^3, there is no indication of external styles. Anterior and posterior cingula extend farther lingually on M^3 than on the preceding teeth and the two are almost united by a median lingual cuspule. Several cuspules are present on the posterior face of M^3 above the cingulum.

M_2 is slightly constricted at the junction of trigonid and talonid but is otherwise nearly quadrangular in outline; the trigonid and talonid are approximately equal in length and width. The trigonid is somewhat higher than the talonid and narrows apically. The protoconid is a large massive cusp that forms nearly half of the trigonid. The heavy, cuspidate paraconid crest runs from the apex of the protoconid to the lingual side of the tooth, where the paraconid is poorly differentiated. The blunt metaconid is but little smaller than the protoconid and equal to it in height; the apices of the two cusps are connected by a papillate crest that is more lightly built than the paraconid crest. Blunt, wrinkled crests run directly lingually and labially down the facing slopes of the protoconid and metaconid. These abut (U.W. no. 1935) or fuse (M.C.Z. no. 8358) to form a third, central transverse crest. A sinuous, antero-posterior cleft partially separates the trigonid apex into labial and lingual halves. All this complicated structure is shallow and would rapidly be obliterated by wear. The posterior face of the trigonid is sloping and bears various small, papillate crests; that behind the metaconid is the most prominent but there is no trace on it of a metastylid. The very large, blunt hypoconid nearly equals the protoconid in size and makes up nearly half of the talonid. The cuspidate crista obliqua is low and fades away toward the base of the talonid. Two minor crests run forward from it to the trigonid base, isolating a very small fossette. The hypoconulid is low but relatively large, and in the

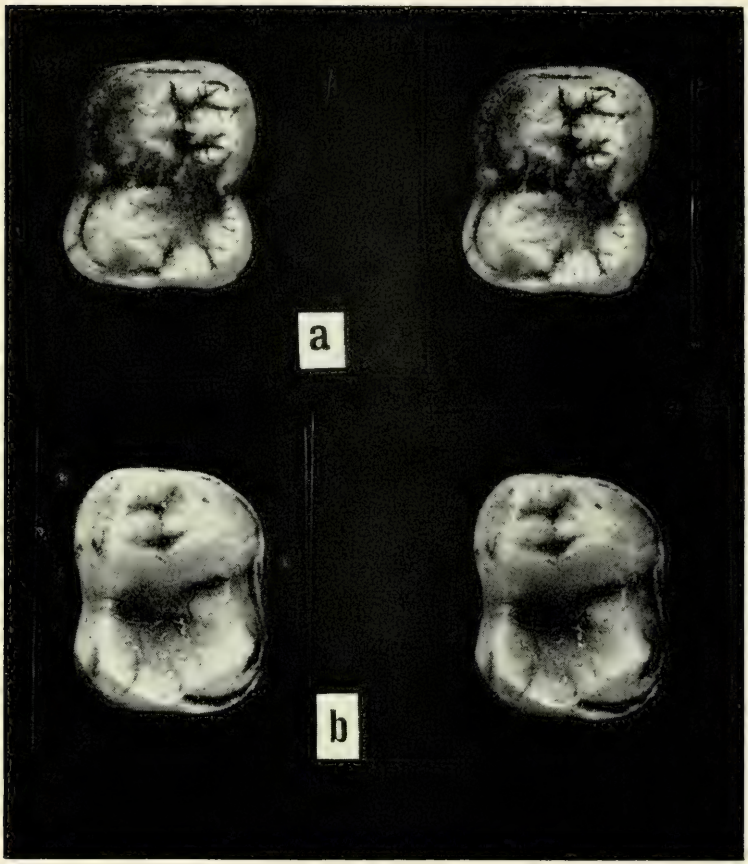

Figure 2. *Colpoclaenus keeferi* gen. et sp. nov. M_2: *a*, U.W. no. 1935; *b*, M.C.Z. no. 8358. X3. Stereoscopic views.

unworn U.W. no. 1935 is tricuspidate and set off from the adjacent cusps by shallow grooves. As is shown by M.C.Z. no. 8358, it is obliterated as a distinct cusp after only a little wear. The entoconid is higher but scarcely larger than the hypoconulid and, like it, at least in U.W. no. 1935, is tricuspidate. From it a cuspidate ridge runs down to the base of the trigonid. The talonid basin is deepest in its anterolingual portion, and the floor bears a number of poorly defined cuspules. A strong, papillate cingulum runs from a point beneath the paraconid around the labial side of the tooth to the hypoconulid; in U.W. no. 1935, but not in

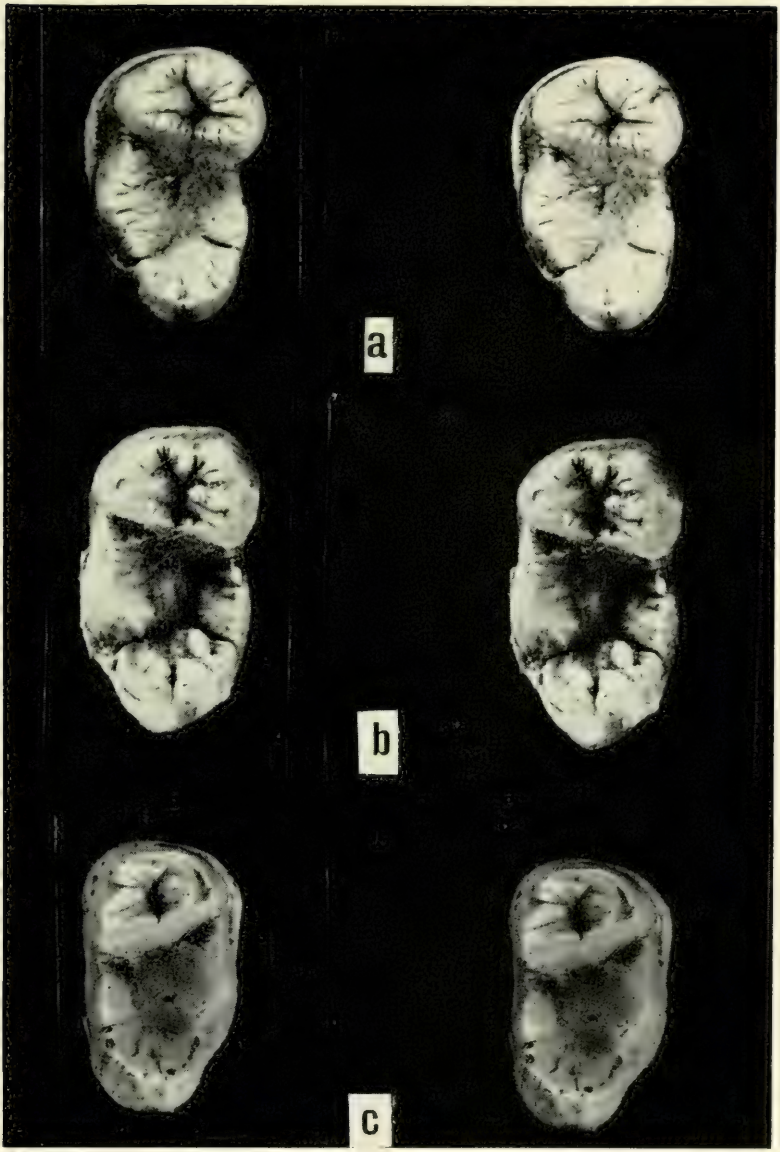

Figure 3. *Colpoclaenus keeferi* gen. et sp. nov. M_3: *a*, U.W. no. 1931; *b*, M.C.Z. no. 8355, type; *c*, U.W. no. 1932. X3. Stereoscopic views.

M.C.Z. no. 8358, this rises to a cuspule in the slight notch between trigonid and talonid.

The third molar is slightly narrower and rather longer than the second; it tapers bluntly toward the rear and, as in M_2, trigonid and talonid widths are approximately equal. The trigonid is shorter and conspicuously higher than the talonid, notably more so than in M_2, tapers apically as on that tooth and is slightly oblique to the long axis, being longer on the lingual than on the labial side. The crown of the trigonid resembles that of M_2 in general, differing in the lesser development of the central transverse crest, which results in the formation of a shallow basin. The posterior face is nearly vertical, with wrinkled enamel. The hypoconid is the largest cusp of the tooth; it is low, blunt, elongate and bears a crest that is bowed laterally. The crista obliqua is lacking in U.W. no. 1931 and is represented only by vestigial, incomplete crestlets in the type and U.W. no. 1932; the hypoconid crest continues on to the base of the protoconid. The broad, flat-crowned hypoconulid is the highest of the talonid cusps and is almost as large as the hypoconid. It is set off by shallow grooves and is itself varyingly grooved and cuspidate. The entoconid resembles that of M_2 both in size and in structure. As on M_2, the talonid basin is deepest antero-lingually and its floor is vaguely cuspidate; it is open anterior to the entoconid due to the absence of a crest on the posterior slope of the metaconid, which on the preceding tooth, together with the entoconid crest, forms a slight dam at this point. The external cingulum runs from the anterior face of the trigonid to the hypoconulid, showing some tendency toward formation of a cuspule between hypoconid and hypoconulid. The tooth is very slightly constricted at the junctions of the trigonid and talonid and of the hypoconulid with the adjacent cusps.

DISCUSSION

We have been able to compare the material referred to *Colpoclaenus keeferi* with specimens representing most of the described arctocyonids. *Colpoclaenus* is a very distinct genus; the combination of characters it presents — summed up in the diagnosis — separates it sharply from all other forms, although certain of them do approach it in one character or another. *Anacodon* resembles it in having accessory cuspules and strongly wrinkled enamel, and also in the possession of three transverse crests on the trigonid, as shown by an unworn M_2 of *A. ursidens* (A.M.N.H.

no. 92). *Claenodon* has moderately wrinkled enamel and comparable crests on the molar trigonids (Gazin, 1956, pl. 7, fig. 5). Other forms — *Thryptacodon*, *Tricentes*, *Mimotricentes*, *Paradoxodon* — have the enamel wrinkled to varying degrees but do not otherwise resemble *Colpoclaenus*. In *Protogonodon* the protocone has a fairly long lingual slope. The trigonid is high in *Oxyclaenus*, *Chriacus*, *Spanoxyodon*, *Prothryptacodon*, and *Metachriacus*. There is a tendency in some of these, especially in *Prothryptacodon*, for the trigonid height to decrease from M_1 to M_3; in *Colpoclaenus* the trigonid is higher on M_3 than on M_2. *Colpoclaenus* thus presents a curious combination of primitive characters, such as high principal cusps in the upper molars, high trigonids in the lowers, and advanced ones, such as a degree of wrinkling of the enamel and proliferation of accessory cuspules that is exceeded only in *Anacodon*. As the family is currently subdivided, *Colpoclaenus* must be placed in the Oxyclaeninae, but its acquisition of arctocyonine-like wrinkling perhaps gives added point to Simpson's suggestion (1937, p. 172) that the Arctocyoninae may be a partially artificial assemblage composed of several lines that were independently following similar adaptive trends.

The last lower molars of *Colpoclaenus* are quite primate-like in general appearance and in some structural details. When our knowledge of the animal was confined to these teeth and to the slightly worn M_2 we were persuaded that we were dealing with a primate astonishingly large for the Paleocene[1]. Recognition of the upper molars rendered such an identification less likely and the finding of the unworn M_2 seems to us to have ended all possibility of it. We wryly sympathize with Cope and with Osborn and Earle who also at times believed an oxyclaenine (*Chriacus*) to be a primate.

Measurements in mm.

	U.W. no. 1933	M.C.Z. no. 8357	U.W. no. 1934
	M^1	M^2	M^3
L	7.1	8.0	6.4
W	11.2	—	8.8

	U.W. no. 1935	M.C.Z. no. 8358	Type, M.C.Z. no. 8355	U.W. no. 1931	U.W. no. 1932	M.C.Z. no. 8356
	M_2	M_2	M_3	M_3	M_3	M_3
L	8.8	9.1	11.2	10.5	10.4	10.9
W	7.0	7.6	6.4	6.3	6.2	6.3

[1] Unfortunately this enthusiasm found fleeting expression on page 9 of the Society of Vertebrate Paleontology News Bulletin No. 61, February, 1961.

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BREVIORA

Museum of Comparative Zoology

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A PICRODONTID INSECTIVORE(?) FROM THE PALEOCENE OF WYOMING

By PAUL O. MCGREW [1]

and

BRYAN PATTERSON

Among the interesting materials found in the course of recent field work in early Tertiary deposits in Wyoming, conducted jointly by the University of Wyoming and the Museum of Comparative Zoology, are several fragments of maxillae and mandibles and a number of isolated teeth of a picrodontid. Only two other records of these problematical little mammals are known: *Picrodus silberlingi* Douglass 1908 from the Fort Union (Lebo) of Montana and *Zanycteris paleocena* Matthew 1917 from the Tiffany of Colorado, the former based on lower, the latter on upper teeth. We confidently assume that our upper and lower molars are referable to the same species. On the evidence of the upper molars this species cannot be placed in *Zanycteris* and on that of the lowers it cannot be excluded from *Picrodus*. We suspect it to be new, but the differences from, and the parts in common with, *P. silberlingi* are so few that we refrain for the present from any attempt at diagnosis. Gazin's tentative record of *Zanycteris* from the Shotgun member of the Fort Union formation in the Wind River Basin (1961, p. 51, and *in* Keefer, 1961) is almost surely based on this form.

The acknowledgments made in a previous paper (Patterson and McGrew, 1962) apply equally to this one, except that the photographs printed here were taken by Mr. John F. Cutler. Abbreviations are as follows: U.W., University of Wyoming; M.C.Z., Museum of Comparative Zoology.

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INSECTIVORA(?)

PICRODONTIDAE Simpson

PICRODUS Douglass

PICRODUS sp. cf. P. SILBERLINGI Douglass

Material: U.W. no. 1780, fragment of left maxilla with M^{1-2}, incomplete alveolus of M^3; M.C.Z. no. 8363, fragment of right maxilla with M^1, incomplete alveolus of M^2; U.W. no. 1781, four complete and three partial M_1; M.C.Z. no. 8422, three M_1; M.C.Z. no. 8423, M_2.

Horizon and localities: Paleocene, early Tiffanian. U.W. no. 1780 is from the Bison Basin Saddle locality, Fort Union formation, E½, sec. 28, T. 27 N., R. 95 W., Fremont Co., Wyoming (Bell, MS.; Gazin, 1956). All the other specimens are from the Shotgun local fauna, Shotgun member, Fort Union formation, ¾ mile SW of the more northerly of the Twin Buttes in the northern part of the Wind River Basin, NE ¼, SE ½, sec. 31, T. 6 N., R. 3 E., Fremont Co., Wyoming (Keefer, 1961; Patterson and McGrew, 1963).

All specimens were encountered in the course of washing operations.

DESCRIPTION

The upper molars of the Wyoming form agree with those of *Zanycteris paleocena* (Matthew, 1917; Simpson, 1935) in basic structure yet differ considerably in detail, especially as regards M^1. This tooth is nearly quadrangular, rather than triangular, in outline, an outpocketing of the posterior cingulum forming a postero-internal angle. The protocone is more anterior in position and more directly internal to the paracone. The protoloph, within which the protocone is completely subordinated, is a heavy, transversely aligned crest that extends almost to the internal base of the paracone, from which it is separated by a shallow notch. The anterior face of the tooth slopes gently upward; the anterior cingulum (double in U.W. no. 1780) is strong compared with that of *Zanycteris*. The antero-external corner of the tooth is rounded and bears no stylar projection. A faint, irregular crest extends, with interruptions, from the base of the protocone to the metacone. It is situated almost wholly within the central basin, of which the lingual and postero-lingual margins are formed by the cingulum. The enamel within

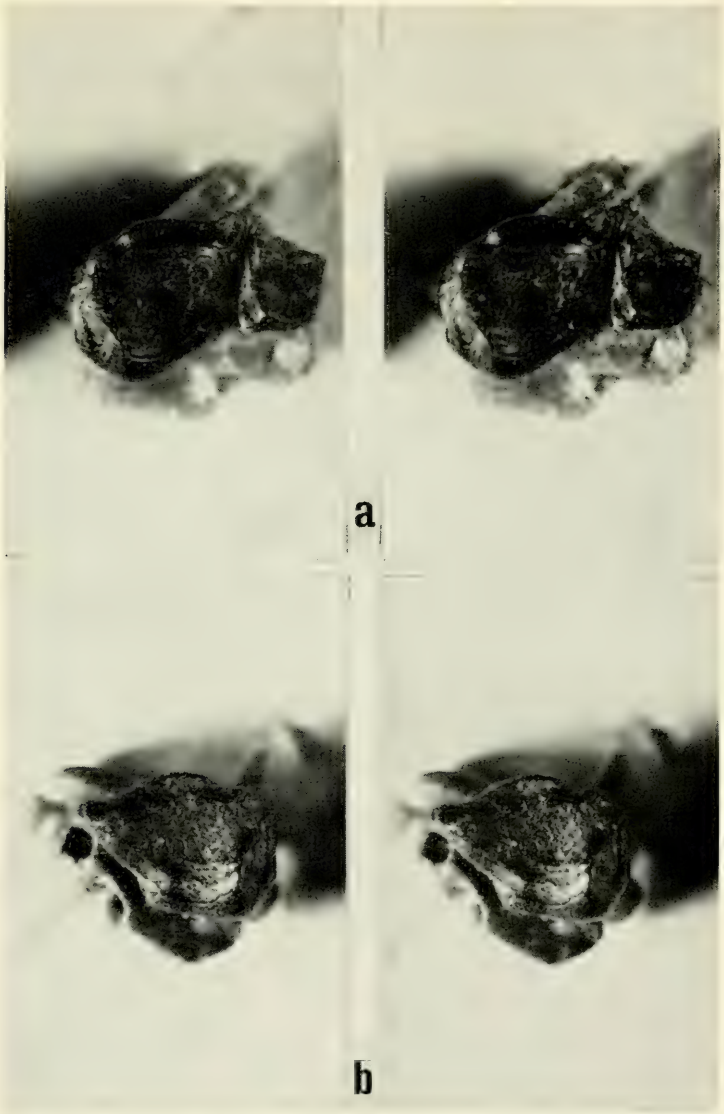

FIG. 1. *Picrodus* sp. cf. *P. silberlingi* Douglass. *a*, U.W. no. 1780, fragment of left maxilla with M^{1-2}. *b*, M.C.Z. no. 8363, fragment of right maxilla with M^1. Approximately X 8. Stereoscopic views.

the area enclosed by the cingulum and the aforementioned low crest is fully as wrinkled as that over the main portion of the central basin. *Picrodus* sp. is rather more advanced than *Z. paleocena* in the essentially complete incorporation of this cingular area into the basin and in the presence of the small postero-internal outpocketing already mentioned.[1] Paracone and metacone are mere elevations at the ends of the long, nearly straight ectoloph. An external cingulum is present posterior to the paracone, where it forms a stout, rather wide and featureless shelf that passes back into the postero-externally projecting metastylar area; a crest connects metastyle and metacone.

M^2 is quite similar to the corresponding tooth of *Z. paleocena*, differing only in a few points. The tooth is slightly smaller relative to M^1, the postero-internal angle is somewhat more squared, and the antero-external style is rather more prominent and connected by a low inconspicuous crest to the tip of the paracone. The adjacent styles of M^{1-2} abut to form an apex from which the outer margin of the cheek tooth series falls away anteriorly and posteriorly.

The first lower molar differs only in detail from that of *P. silberlingi*. The paraconid is usually higher and slightly more independent and is invariably larger than the metaconid. In several teeth the latter cusp has almost or quite lost its identity in the oblique trigonid crest. Trigonid and talonid are consistently better demarcated externally. The crest that forms the external border of the talonid curves inward at its anterior extremity to reach the center of the posterior face of the trigonid a short distance below the protoconid rather than abutting against the base of the trigonid externally, as is the rule in *P. silberlingi*. A narrow, shallow groove lies between the trigonid face and the incurving position of the crest. The main portion of the talonid crest, that forming the lateral and posterior borders of the basin, appears to be more cuspidate than in the Lebo sample; the cuspules number from four to nine rather than from two to three. The two cuspules on the lingual side of the talonid are extremely variable in the Shotgun sample, amounting in some specimens to little more than irregularities on the talonid margin. An interradicular crest is present. M_2 resembles the corresponding tooth of *P. silberlingi* more closely than does M_1; Simpson's description (1937, p. 138) applies practically verbatim to our single specimen.

[1] The posterior cingulum of M^1 of *Zanycteris paleocena* is not as distinct from the dentral basin as Simpson's figure (1935, fig. 6) would suggest.

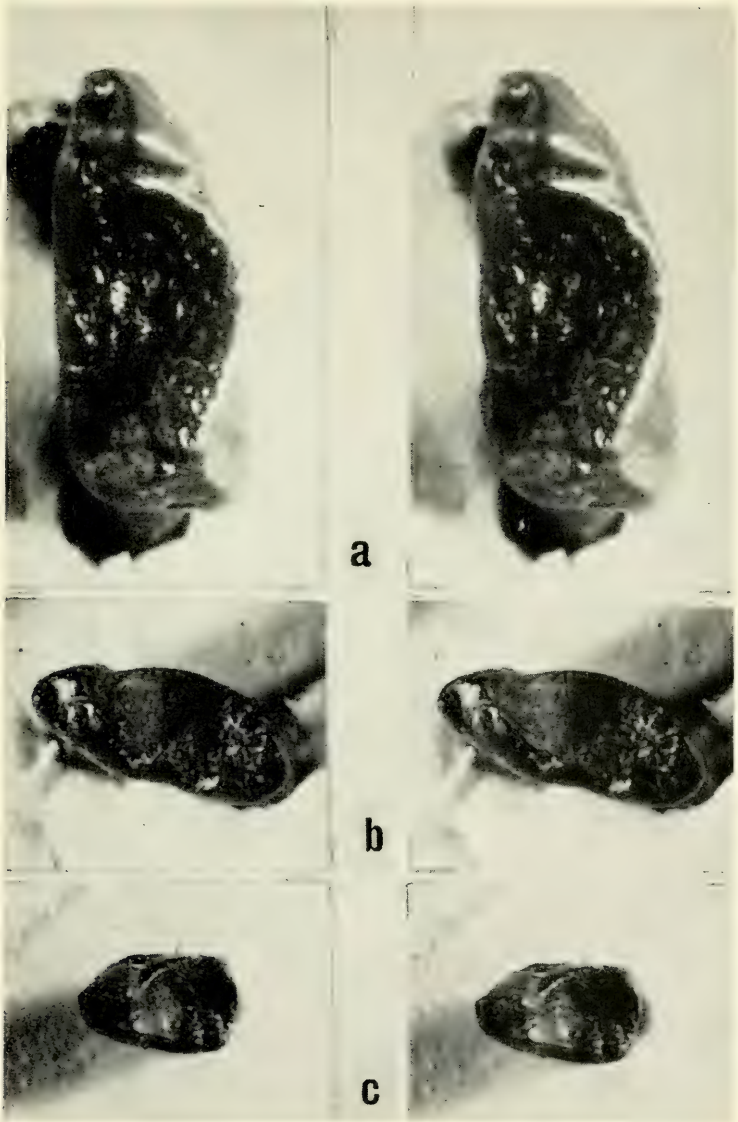

FIG. 2. *Picrodus* sp. cf. *P. silberlingi* Douglass. *a*, U.W. no. 1781, RM_1, approximately X 20. *b*, M.C.Z. no. 8422, RM_1, approximately X 11. *c*, M.C.Z. no. 8423, RM_2, approximately X 11. Stereoscopic views.

In both upper and lower molars, the enamel at the base of the crown extends out far beyond the necks of the teeth, the external and posterior cingula of M^1 and the postero-external portion of the talonid of M_1 being especially projecting. The term exoedaenodont has been applied to this condition, which, in the Insectivora, is encountered especially among the Dimylidae (Hürzeler, 1944). Hürzeler and also Saban (1958, p. 896 n) believe that exoedaenodonty is an indication of a malacophagous diet, Saban citing in support the numerous shells of *Anodonta* that occur in deposits that yield remains of Dimylinae. However this may be for dimylids with their strongly cusped molars, we do not believe that it indicates any such habit for the picrodontids.[1] As Matthew recognized in his description of *Zanycteris*, low crowned more or less flattened molars with finely wrinkled enamel of the sort that occur in the family almost certainly indicate a frugivorous diet.

The small fragments of maxillae and mandibles add nothing to knowledge except to suggest that the anterior root of the zygoma may not have been as stout as in *Zanycteris*.

MEASUREMENTS IN MM.

	U. W. 1780	M.C.Z. 8363
Length M^1	2.85	2.95
Width M^1	2.35	2.40
Length M^2	1.35	—
Width M^2	1.63	—

	N	OR	M	σ	V
Oblique maximum diameter[2] M_1	7	2.40 —2.85	2.66 ±.051	.135 ±.036	5.07 ±1.35
Width talonid M_1	10	1.00 —1.40	1.16 ±.0386	.122 ±.027	10.5 ±2.34

	M.C.Z. 8423
Length M_2	1.90
Width M_2	1.10

[1] Nor, *a fortiori*, for such forms as soricids and various microchiropterans that are exoedaenodont to varying degrees.

[2] As measured by Simpson (1937, p. 138).

DISCUSSION

Matthew, in his description of *Zanycteris paleocena*, took no account of *Picrodus silberlingi*, and indeed there was nothing in Douglass' description and figures to invite comparison between the two forms. It remained for Simpson, with new material of *P. silberlingi* and first-hand knowledge of *Z. paleocena*, to show that they were closely related. As he pointed out (1937, p. 136), the species were distinct, but in the absence of comparable parts it could not certainly be stated that this was also true of the genera. We now have lower molars indistinguishable generically from *Picrodus* found with upper molars clearly distinct from those of *Zanycteris*. On the face of it, then, the two previously described species would appear to belong to distinct genera. However probable, this cannot yet be considered as certain. The highly specialized lower molars may perhaps prove to be rather stereotyped within the family and hence unreliable for generic discrimination. Although quite unlikely, it is thus still conceivable that *P. silberlingi* and *Z. paleocena* may represent one genus, and *P.* sp. another. Finds of associated upper and lower teeth of the previously described forms will be required before all doubt on this score can be set at rest.

As regards the broader question of picrodontid affinites, we are in complete agreement with Simpson (1937) that the family cannot be referred to the Chiroptera. The enlarged lower incisor, small upper canine, small premolars, long and slender muzzle, and origin of the anterior root of the zygoma opposite M^{1-2} are definitely non-chiropteran characters. Since Matthew's work, it has always been stated that the molars resembled those of the specialized Phyllostomatidae, members of the subfamilies Sturnirinae, Phyllonycterinae and Stenoderminae. Thanks to the excellent collection of bats in the Museum of Comparative Zoology, we have been able to make comparisons with nearly all members of these three groups. We are quite unimpressed by the resemblances between their molars and those of the picrodontids. Essentially these are limited to wrinkled enamel and pointed trigonids, and are more than offset by numerous differences.

Sturnira and the Phyllonycterinae have smooth enamel. In *Sturnira*, the upper molars have deep, antero-posteriorly running central valleys and no traces of lophs; the lowers have the trigonid and talonid basins confluent, the metaconid widely separated from the protoconid, and the trigonid of M_1 neither compressed nor elevated. In the phyllonycterines, the upper molars

are triangular and lack lophs and a stylar area; the lowers have the trigonids scarcely elevated above the talonids, and all cusps, save the protoconid of M_1, incorporated in the rims of the talonid basins. The Stenoderminae have wrinkled, often strongly wrinkled, enamel, but the molar structure is very different from that of the picrodontids. The upper molars are short in comparison with their widths, M^2 is large (except in *Pygoderma*), frequently larger than M^1, and the paracones and metacones are high and trenchant (in *Pygoderma* the paracones only), standing well above the flattened lingual portions of the teeth. The trigonids are elevated and compressed to points, but the compression does not involve the whole trigonid as it does in the picrodontids. The metaconid, when not subordinated in the crest running to the apex of the protoconid, is a distinct element situated low on the crown. The pointed protoconids of both molars and premolars give every appearance of being involved in the same morphogenetic gradient.

The few resemblances in molar structure between picrodontids and specialized phyllostomatids seem clearly to be of the sort brought about by convergence. The Microchiroptera can be eliminated as possible relatives of the Picrodontidae, and we can see in the latter nothing suggestive of the Megachiroptera. On the positive side, we can offer no really useful suggestion as to the ordinal affinities of the picrodontids. Simpson has remarked that "reference to the Primates is merely a possibility, with no positive evidence to commend it." The possibility, of course, exists, and such picrodontid characters as the small size of the trigonid compared with that of the talonid and the tight grouping of the trigonid cusps could be cited as resemblances, however vague, to early members of that order. Resemblances of this sort scarcely constitute positive evidence, however. Reference to the Insectivora is equally unsatisfactory. Our queried placement of them there is strictly faute de mieux, due largely to reluctance to use the Primates as a scrap-basket order.

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BREVIORA

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ON THE RACES OF *KINIXYS BELLIANA* GRAY

By R. F. LAURENT

Museum of Comparative Zoology

When I noticed the peculiarities of *Kinixys belliana* from northeastern Congo, I suspected that these populations might represent a race already described by Rüppell under the name of *schoensis*, but I did not have Rüppell's description. Dr. Mertens kindly gave me the necessary information and it became evident that these populations were different from *schoensis*, and I therefore described the race *mertensi* (1956). Dr. Mertens (*in litt.*) declared that *schoensis* was in his opinion a valid race, but he apparently changed his mind, since the rehabilitation of *schoensis* has never appeared (Wermuth and Mertens, 1961). In preparation for a checklist of the turtles of Africa, I have now reinvestigated the validity of *schoensis* and also the range of *mertensi* toward the east and northeast.

Acknowledgments. I wish to thank Miss A. G. C. Grandison (British Museum of Natural History) and Mr. A. Opdenbosch (Technician in the Musée Royal de l'Afrique Centrale, Tervuren) who very kindly gave me invaluable information on specimens in their charge. My thanks are due also to Prof. G. G. Simpson for advice on statistical matters and to Dr. E. E. Williams for reading the manuscript and helpful criticisms. This study has been supported by National Science Foundation grant NSF G 17144.

KINIXYS BELLIANA Gray

This paper limits itself to the examination, with the aid of the ratios already used in the description of *mertensi*, of two questions: (1) Is *schoensis* Rüppell recognizable as a northeastern race, and (2) does *mertensi* connect with the typical form by a smooth cline in which no objective limits could be formulated for the eastern distribution of the race?

Measurements, additional to those taken for the description of *mertensi* (1956) (i.e. on other specimens), were taken on the MCZ specimens; Miss A. G. C. Grandison, with her customary kindness, sent the pertinent measurements for specimens from northeastern Africa and Uganda. Mr. A. Opdenbosch furnished also data on a large series of *K. belliana* from the Congo.

Admittedly, the method of relying on other persons to take measurements has serious drawbacks since it can introduce bias in the data. For amphibians the discrepancies are very great indeed, but as far as turtles are concerned it has been hoped that the measurements are generally so easily definable that these discrepancies would be almost negligible. However, the comparison of the ratios already published (Laurent 1956) with those calculated on Opdenbosch's measurements disclosed a considerable bias in the breadth of the carapace (maximum breadth, and breadth on level of lateral ends of humero-pectoral sutures). Even disregarding these data, the variation of *belliana* is such that the validity of *schoensis* appears untenable on present evidence. [Of course, other characters may prove some day that the northeastern populations or even some others from east or southern Africa are subspecifically differentiated.] Thus, in regard to the four ratios used in my previous work (Laurent 1956) the situation is as follows.

1. From the data at hand in 1956, the general shape of the carapace seemed definitely different in *mertensi* and "*schoensis*" and *belliana*. The carapace breadth (at the level of the lateral ends of the humero-pectoral suture) in per cent of the maximum breadth (back part of the carapace) was 87.2 to 97.8 ($m = 92$ for nine specimens) for *belliana*, 78.7 to 90.3 ($m = 85.67$ for fifteen specimens) for *mertensi* and 83.8 for the type of *schoensis*. The overlap was slight enough to make unnecessary any test for significance of the difference. However, the data now at hand are definitely less conclusive. The difference seems to be still statistically significant between *mertensi* and the complex of populations from eastern and southern Africa which we call *belliana* but which surely cannot be considered as homogeneous. Also, because bias is obvious in these rather difficult measurements and because other differences are more clearcut, it has not been found worthwhile to make any statistical calculations. The specimens from Sudan, Abyssinia and Somaliland do not appear to be significantly distinct from those from East Africa, though more

consistent measurements taken on more numerous specimens could some day disclose a valid difference.

2. In my 1956 work the ratio between the median gular suture plus the median humeral suture and the breadth of the plastron at the level of the lateral ends of the humero-pectoral sutures was seen to show a very clearcut difference between *belliana* and *mertensi* — the figures being 56.7 to 73.3 ($m = 66.87$) for *belliana* ($N=9$), 72.9 to 91 for *mertensi* ($N=15$). The new data are *ana* ($N=9$), 72.9 to 91 ($m=84.92$) for *mertensi* ($N=15$). The new data are still reliable as the measurements are not likely to suffer from individual bias. The ratios now obtained are as follows (expressed in percentage):

a) *belliana* ($N = 87$) 49.5-82.8 $m = 66.45$ $v = 12.51$
b) *mertensi* ($N = 22$) (57)[1] 75-94 $m = 84.18$ $v = 12.47$
c) *"schoensis"* ($N = 8$) 55.7-71.7 $m = 69.13$ $v = 10.80$
d) *nogueyi* ($N = 3$) 65.4-73-83.1

The variation coefficients are high because the samples are heterogeneous from the point of view of size and consequently of age. In the *mertensi-belliana* and *belliana-"schoensis"* comparison, Student's t is respectively 8.45716 and 8.25106, which shows highly significant differences in view of the small number of specimens.

3. The ratio between the pectoral suture and the sum of the gular and humeral sutures gives the following figures:

a) *belliana* ($N = 87$) 25.6-69 $m = 42.01$ $v = 18.30$
b) *mertensi* ($N = 21$) 0-31 $m = 19$ $v = 41.51$
c) *"schoensis"* ($N = 8$) 31.4-42.3 $m = 34.50$ $v = 9.86$
d) *nogueyi* ($N = 3$) 27.8-27.8-39.1

Notwithstanding an enormous variation coefficient in *mertensi*, t shows a significant difference between *mertensi* and *"schoensis"* ($t = 5.32$) and *mertensi* and *belliana* ($t = 12.71$) but not between *belliana* and *"schoensis."*

4. The ratio between the pectoral and the abdominal sutures gives the following figures:

a) *belliana* ($N = 86$) 21.3-60 $m = 39.89$ $v = 25.81$
b) *mertensi* ($N = 21$) 0-31.2 $m = 18.71$ $v = 42.98$
c) *"schoensis"* ($N = 8$) 29.4-37.4 $m = 33.5$ $v = 8.62$
d) *nogueyi* ($N = 3$) 22.4-36

[1] The low figure 57 comes from a juvenile.

Only the difference between "*schoensis*" and *mertensi* proves to be significant with a t of 5.03.

Two other ratios not previously used but combining the same measurements have proven useful.

1. The ratio between pectoral suture and the maximum width of the carapace:

a) *belliana* ($N = 87$) 11.3-24 $m = 16.51$ $v = 18.50$
b) *mertensi* ($N = 21$) 0-13.8 $m = 8.95$ $v = 41.87$
c) "*schoensis*" ($N = 7$) 11.6-15.3 $m = 12.86$ $v = 13.83$

Student's t is significant between *belliana* and *mertensi* (9.48), and between "*schoensis*" and *mertensi* (6.65), dubiously significant between *belliana* and "*schoensis*" (3.11).

The same relation between *belliana* and "*schoensis*" becomes, however, significant if analyzed by regression lines ($t = 4.26$).

2. The ratio between the width of the plastron at level of the lateral ends of the humero-pectoral suture and at the abdominal suture:

a) *belliana* ($N = 86$) 110-200% $m = 145.45$ $v = 11.30$
b) *mertensi* ($N = 21$) 103-147% $m = 114.52$ $v = 31.54$

Student's t (8.05) is highly significant.

As a result of these computations, *mertensi* appears definitely valid, but "*schoensis*" seems to be so only for two ratios: 1. the ratio of the sum of humeral and gular sutures to the breadth of the plastron at the level of the humero-pectoral suture and 2. the regression line for the correlation between the length of the pectoral suture and the maximum breadth of the carapace.

From a taxonomic point of view, it does not seem advisable to revive "*schoensis*" on such slender evidence — more especially as the *belliana* sample is geographically highly heterogeneous. A complex clinal variation from Rhodesia to Ethiopia is possible, since we have no data from the populations between Kenya and Ethiopia or Eritrea. Some records from Eritrea (Sordelli 1901, Calabresi 1927, Scortecci 1928) disclose a shortening of the pectoral suture, as in *mertensi*.

On the other hand, no east-west cline exists between *mertensi* and *belliana:* the British Museum specimens from Entebbe and Mount Elgon are clearly *mertensi*.

The two questions propounded have thus the following answers:

(1) A race "*schoensis*" cannot now be revived for the northeastern populations of *Kinixys belliana*.

(2) The distribution of *Kinixys belliana mertensi* includes Uganda, but its northern limit remains unknown.

These conclusions are still provisional. More material could prove not only that "*schoensis*" is valid but that other subspecies can be recognized, or on the contrary that even *mertensi* merges in *belliana* through Sudanese and Abyssinian populations.

Material examined

Kinixys belliana belliana Gray

MUSEUM OF COMPARATIVE ZOOLOGY: *Sudan:* Torit (1). *Kenya:* Golbanti (1), Ithanga Hills (1), Kibwezi (1), Voi (5). *Tanganyika:* Amboni (1), Kilosa (1), Kiponda to Mitungu (1), Kitaya (1), Mikindani (4), Morogoro (1), Simo near Tabora (2), Turiani (1), Ujiji (2). *Zanzibar Island:* Zanzibar (1). *Nyasaland:* Cholo Mtn. (1), Mtimbuka (5). *Northern Rhodesia:* Isoka (1). *Southern Rhodesia:* Birchenough Bridge (1), Bulawayo (1), Hot Springs (2), Lumani (1), Selinda Mtn. (3), Umtali (1). *Transvaal:* Naauwpoort (1). *Katanga:* Kapiri (1), Lukafu (1).

BRITISH MUSEUM (NATURAL HISTORY): *Sudan:* Kadugli (1). *Ethiopia* (1), Anseba (2). *Somaliland:* Berbera (1), near Berbera (1).

MUSÉE ROYAL DE L'AFRIQUE CENTRALE (Tervuren, Belgium). *Kenya:* Kibwezi (1), Voi (1). *Northern Rhodesia:* Abercorn (3). *Katanga:* Kabambaie (1), Kabinda (1), Kakanda (3), Kansenia (12), Kapiri (8), Lofoi sources (1), Lukafu (2), Lukonzolwa (4), Mwera (1), Ste. Walburge (2). *Kivu:* Makunga (2).

Kinixys belliana mertensi Laurent

MUSEUM OF COMPARATIVE ZOOLOGY: *Ituri:* Mahagi-Port (1).

BRITISH MUSEUM (NATURAL HISTORY): *Uganda:* Entebbe (1), Mt. Elgon (2).

MUSÉE ROYAL DE L'AFRIQUE CENTRALE (Tervuren, Belgium). *Congo,* without locality (4). *Uele:* Dika (3), Mauda (1), Niangara (1). *Ituri* (1): Abimva (1), Gangala na Bodio (3), Mahagi-Port (3). *Stanleyville District:* Avakubi (1).

Kinixys belliana nogueyi Lataste.

MUSEUM OF COMPARATIVE ZOOLOGY: *Dahomey:* Bassila (1). *Togo:* Tohoun (1). *Sierra Leone:* Kabala (1).

Two specimens from Lukolela (western Congo: M.A.C. 4648)[1] and from the Kwango District (southwestern Congo: M.A.C. 10736) suggest that a differentiated population exists in the lower Congo region, which somewhat resembles *mertensi* in having a short pectoral suture and a long abdominal suture. Other specimens are, of course, needed.

Key to the races of Kinixys belliana

A. Forelimb with 4 claws — Range: Western and northern Cameroon, west to Senegal. ..... *K. b. nogueyi* Lataste

B. Forelimb with 5 claws (occasional specimens have 4 claws)

1—Ratio between the median gular suture + the median humeral suture and the breadth of the plastron at the level of the lateral ends of the humero-pectoral sutures: 75 to 94% (less than 75 in juveniles). Ratio between the pectoral suture and the sum of the gular and humeral sutures: 0–31%

Range: Northeastern Congo and Uganda (presumably also République Centre Africaine and eastern Cameroon).

..... *K. b. mertensi* Laurent

2—These ratios, respectively, 49 to 83% and 25 to 69%.

Range: Sudan east to Eritrea and Somaliland, south to Natal, northwest to Angola and southern Congo.

..... *K. b. belliana* Gray

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[1] M.A.C.: Musée Royal de l'Afrique Centrale (Tervuren).

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RHIPIDISTIAN CLASSIFICATION IN RELATION TO THE ORIGIN OF THE TETRAPODS

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INTRODUCTION

In an extensive study of the nasal region of the lower gnathostomes, Jarvik (1942) concluded that the four families of rhipidistian Crossopterygii represent two distinct stocks (superorders according to Lehman, 1959) — the 'Porolepiformes' (Porolepidae and Holoptychidae) and the 'Osteolepiformes' (Osteolepidae and Rhizodontidae). Of major interest to students of vertebrate evolution was his conclusion that the structures seen in the snout of 'Porolepiformes' were closely comparable to those seen in the recent Urodela, and those of 'Osteolepiformes' were comparable to those of the recent Anura, and that here was evidence of a biphyletic origin of the tetrapods. His work was based upon detailed studies of two genera, *Porolepis* and *Eusthenopteron* (a rhizodontid). Jarvik's material was unusual in that it showed details of the endocranial part of the snout which it is not usually possible to study in fossil crossopterygians; in recent years, however, more such material has been described (Vorobjeva, 1959, 1960a, 1960b; Kulczycki, 1960) and Ørvig (1957) has published a full treatment of the interrelations of the Rhipidistia on the basis of the structure of the scales. For the last year or so I have been engaged in a study of the ethmoid region of the osteolepids *Megalichthys* and *Ectosteorhachis*, continuing the work started by Romer (1937, 1941).

Briefly, the newly available evidence does not support all of Jarvik's original conclusions. Because of the relation of this

work to the problem of the origin of the tetrapods and particularly to the currently disputed theories of the ancestry of the recent Amphibia, I have decided to publish this short review of the more pertinent points in advance of a more thorough treatment. This may also be useful since the work of Vorobjeva, being in Russian, may not be readily available to everyone.

This paper forms part of the work to be submitted to the Department of Biology, Harvard University, in fulfillment of the requirements for the degree of Doctor of Philosophy; it is my pleasure to acknowledge the constant help and guidance of Professor A. S. Romer during all this study; he and Dr. E. E. Williams and Professor B. Patterson read and criticized the manuscript. I am also grateful for the friendly encouragement of Drs. Jarvik and Ørvig in Stockholm; the former has allowed me to see an as yet unpublished manuscript on this subject (Jarvik, in press). My friend Mr. Simon Karlinsky provided the translations from the Russian. My studies have been supported by the award of N.A.T.O. Science Studentship 3/60/955 by H. M. Department of Scientific and Industrial Research, London, and by the Jeffries Wyman Scholarship at Harvard University.

MATERIAL

It is necessary to establish the taxonomic status of certain of the rhipidistians concerned in this study; these are:

Megalichthys Agassiz 1841 (including *Ectosteorhachis* Cope 1880). Carboniferous and Lower Permian of Europe and North America.

Platycephalichthys Vorobjeva 1959. Upper Devonian of U.S.S.R.

Panderichthys Gross 1941. Upper Devonian of U.S.S.R.

Porolepis (*P. ex grege posnaniensis* [Kade 1858]). Lower Devonian of Poland.

Megalichthys-Ectosteorhachis. *Ectosteorhachis* was originally described by Cope (1880) from material from the Lower Permian of Texas; it was later (1891) referred by him to the Carboniferous genus *Megalichthys.* In recent years it has been suggested several times (see, for example, Romer, 1941) that the two genera are, in fact, distinct and that the Lower Permian material will have to be referred back to *Ectosteorhachis.* No formal diagnosis of this has been given; however, in advance of

such a diagnosis I shall follow precedent and refer to the Permian fish, for convenience, as '*Ectosteorhachis.*'

Megalichthys and *Ectosteorhachis* are generally acknowledged to be members of the Osteolepidae. Berg (1958) unites them with Owen's *Parabatrachus* to form the separate family Parabatrachidae; however, available evidence, e.g. Bystrow (1950), shows that *Megalichthys* is closely related to *Osteolepis* itself.

Porolepis. Kulczycki's (1960) material of *Porolepis* is without doubt correctly referred to that genus.

Platycephalichthys and *Panderichthys.* These genera are involved in a long series of taxonomic shufflings concerning the genera *Cricodus, Dendrodus* and *Polycodus;* they may be considered most conveniently together. The best way to review the situation seems to be to start with the description by Rohon (1889) of several specimens from the Upper Devonian of Russia, some of which he assigned to *Dendrodus biporcatus* Owen (Rohon, 1889, plate 1, figures 1, 5, 9, a skull, and 2, 7 8, a tooth and two scales), while others he named *Cricodus wenjucovi* (Rohon, 1889, plate 1, figures 4, 6, a skull from the River Ojatj, and 3, 11, a skull and lower jaw from the River Sjass). Since these specimens are not given numbers by Rohon, I shall refer to them, for convenience, by the number of the figure by which they are illustrated.

Gross (1933) placed those specimens figured in plate 1, figures 1, 3, 4, 5, 6, 9, together with new material from the Baltic Old Red Sandstone, in the genus *Polyplocodus* Pander 1860, as the new combination *Polyplocodus wenjucovi.* Jarvik (1937), however, put "figures 1, 3, 4, 5, 6, 9, 11" in *Eusthenopteron* as *E. wenjucovi.* He also concluded that the names *Cricodus, Dendrodus,* and *Polyplocodus* should not be assigned to any fresh material because of the fragmentary and enigmatic nature of the originals. Hence Gross (1941) named a new genus *Panderichthys* in order to reassign material named by him (1930) *Polyplocodus* (*Cricodus*) *rhombolepis* (see also Gross 1933, 1936). Now there enters a possible source of confusion because Gross (1941) named a second new species — *Panderichthys bystrovi* — for the material from the Baltic Old Red which he had named *Polyplocodus wenjucovi* in 1933 (see above), while leaving the Rohon material in *Eusthenopteron wenjucovi.* Vorobjeva (1960a) named a third species — *Panderichthys stolbovi.*

In 1959 Vorobjeva described a new genus *Platycephalichthys*, with the type *Platycephalichthys bischoffi*, based on recently collected material from the Upper Devonian of Russia, and included in this genus the Rohon specimen from River Ojatj ("figures 4 and 6") as a new species *Platycephalichthys rohoni*. Later (1960b) she referred the remaining Rohon material to *Eusthenodon* Jarvik 1955 as *Eusthenodon wenjucovi*.

Thus the two genera now comprise:

Panderichthys

P. rhombolepis Gross 1941

P. bystrovi Gross 1941

P. stolbovi Vorobjeva 1960

Platycephalichthys

P. bischoffi Vorobjeva 1959

P. rohoni Vorobjeva 1959

From the structure of the scales and teeth, *Platycephalichthys* is a member of the Rhizodontidae. *Panderichthys* was assigned by Gross (1941) to the Rhizodontidae but there seems little doubt (Vorobjeva 1960a, and Ørvig 1957) that it should be placed with the Osteolepidae.

SUBDIVISION OF THE RHIPIDISTIA

Jarvik (1942, p. 489) lists a series of differences between *Porolepis* and *Eusthenopteron* which he considers to be representative of a basic split within the Rhipidistia. He also (1942, pp. 417, 495) discusses the connections between these fishes and the recent Amphibia. In general, the same characters are involved in the two arguments. In the next few pages I shall review recent findings which indicate that certain of these characters no longer support Jarvik's distinctions. These are all characters which may readily be determined in the fossils; this is in contrast with some of Jarvik's points involving the passage of nerves and vessels, the refutation of which could be as difficult as their interpretation. Some of Kulczycki's (1960) statements may be disputed, as I shall mention later, on the grounds that his material was insufficiently well preserved. This criticism cannot apply to Vorobjeva's work, particularly since the most important of the characters she has described are, as already mentioned, easily ascertained.

The recognition, in certain anatomical characters, of resemblances between specific rhipidistians and recent amphibians, without the supporting evidence of a fossil lineage (lacking in

the case of the Urodela and Anura) becomes, to a certain extent, a matter of subjective judgment. In the following pages I shall consider primarily the evidence for a basic distinction between 'Osteolepiformes' and 'Porolepiformes,' for it is upon the validity of this supposed dichotomy that all subsequent phylogenetic hypothesis must rest.

The nature of the anterior palatal fenestrae. According to Jarvik (1942, p. 489, etc.), an important difference between the 'Osteolepiformes' and the 'Porolepiformes' lies in the nature of the paired palatal recesses present between the anterior edges of the vomers and the posterior rim of the premaxillae. In *Eusthenopteron* this region has the form of a shallow, partially sub-divided groove, the 'prenasal groove,' limited posteriorly by the edges of the vomers; in *Porolepis* there is a pair of 'pits' extending backwards between and separating the vomers. These palatal recesses which are described by three names — 'fossae apicales,' 'anterior palatal fenestrae,' and 'pre-nasal pits' — were assumed by Jarvik to have contained glandular organs homologous with the various intermaxillary glands of recent Amphibia. It was further proposed that the condition in *Eusthenopteron* foreshadowed that of recent Anura, and the condition in *Porolepis* that of Urodela.

It had already been suggested, however, that these recesses served solely to receive the points of large tusk-like teeth set in the tips of the lower jaws (Holmgren and Stensiö, 1936; Romer, 1937; and now also Kulczycki, 1960). The material at my disposal shows quite clearly that this latter explanation is the true one for the Osteolepidae. Plate I shows the tusk fitting into the palatal recess, leaving no room for any glandular structure. That this is also the case in other 'Osteolepiformes' may be deduced from the similar large tusks of the lower jaws — for example, in *Panderichthys* (Gross, 1941). In 'Porolepiformes' the situation is very similar, but in this case, as Jarvik has shown, the teeth concerned are a pair of tooth whorls. This extremely interesting discovery provides, incidentally, positive indication that the familiar *Onychodus*, long known from such tooth whorls, is, in fact, a 'porolepiform' rhipidistian (Jarvik, in press).

The presence of the paired tooth whorls speaks, indeed, for the unity of the 'Porolepiformes,' but the morphological relationship between the type of palatal fenestra and the lower jaw dentition completely precludes any phylogenetic relationship

between the fenestrae in Rhipidistia and the glandular organs of recent Amphibia.

Evidence from the cranial cavity. A point of resemblance, apparently possible of interpretation as evidence of relationship, between *Porolepis* and the Urodela is that in both ". . . the internasal wall is broad and does not form any nasal septum. It lodges the ethmoid part of the cranial cavity" (Jarvik, 1942, p. 417). This, moreover, is supposed to be in direct contrast with the 'Osteolepiformes' (and Anura) — by extrapolation from the situation in *Eusthenopteron* in which the internasal wall is relatively narrow and also solid.

Kulczycki (1960) noted that his material of *Porolepis* did not show any forward extension of the cranial cavity between the nasal sacs; his material was perhaps not as good as might be desired fully to substantiate this view, since it consisted entirely of natural casts and not true bony remains. At the same time that Kulczycki's work was published there appeared the work of Vorobjeva. Her material consisted of several portions of the skulls of *Platycephalichthys* and *Panderichthys,* both of which are undoubtedly 'osteolepiform' and both of which, she states, have an ethmoid extension of the cranial cavity. Her description of *Platycephalichthys* is interesting; ". . . *a wide internasal portion* (of the braincase) *with a cavity stretching forward almost to the front edge of the skull*" (Vorobjeva, 1960a, trans.).

In the face of evidence that a rhizodontid and an osteolepid have a 'pars ethmoidalis cranialis' and at least one species of *Porolepis* may not, one is forced to conclude that this character is of no significance in any attempt to distinguish supra-familial groupings within the Rhipidistia. One may further bear in mind that the extent of the cranial cavity need have no relation to the extent of the brain contained therein. A dramatic demonstration of this is afforded by the coelacanth *Latimeria* (Millot and Anthony, 1958), in which a large cranial cavity contains but a small brain. Presence or absence of the pars ethmoidalis cranialis is thus a rather labile character in the Rhipidistia and, having no great anatomical or functional basis, no phylogenetic speculation may reasonably be drawn from it.

Nasal apertures and the nasal cavity. All known 'Porolepiformes' are characterized by the presence of two external nares and a choana. Further, the endocranial opening for the posterior naris is confluent with that for the choana. In *Eusthenopteron,* on the other hand, there is but one external naris and this

is separated from the choana by the lamina nario-choanalis of the endoskeletal nasal capsule. Until the work of Vorobjeva this was believed to hold true for all 'Osteolepiformes' but *Panderichthys* is described (Vorobjeva, 1960a) as having both an anterior and a posterior external naris. From her figures it is not possible to determine whether the described confluence of the posterior naris with the fenestra endochoanalis is due merely to a defect in the preservation or not. This is indeed a strange situation for a fish which is in all major respects to be considered 'osteolepiform.'

Jarvik has other speculations based on the detailed configuration of the nasal cavity itself, but these seem to be more open to dispute in connection with phylogenies spanning 300 million years. *Ectosteorhachis* certainly lacks most of the ridges, grooves and depressions described in *Eusthenopteron* and supposed to be typical of all 'Osteolepiformes.'

Jarvik described in *Eusthenopteron* a foramen in the post-nasal wall which he states is the posterior endonarinal fenestra (Jarvik's terminology). This is also present in *Ectosteorhachis*, but the presence of an anterior naris in *Panderichthys* may possibly indicate that the single external naris of 'Osteolepiformes' is homologous with the posterior naris of *Porolepis*. In this case the foramen in the post-nasal wall, which Jarvik considers to be the forerunner of the tetrapod naso-lachrymal duct, may possibly have to be interpreted in some other fashion, but considerably more evidence is needed to settle this point.

Other structures. There are several other points, noted by Jarvik as indicative of a division within the Rhipidistia, which are contradicted by the anatomy of *Ectosteorhachis:*

1) Jarvik (1942, p. 492) states that a difference between 'Osteolepiformes' and 'Porolepiformes' is that in the former the vomers are in mesial contact, while in the latter they are separate from each other. Although in the sectioned material at my disposal the vomers are slightly displaced, it seems that these bones are not in mesial contact. Further, they lack the posterior extension passing back on either side of the tooth-bearing part of the parasphenoid, which has also been stated to be typical of 'Osteolepiformes.' The vomers are thus much more similar to those of *Porolepis* than to those of *Eusthenopteron;* they lie entirely anterior to the tooth-bearing part of the parasphenoid.

2) Jarvik states (1942, p. 492) that in 'Osteolepiformes' the parasphenoid is narrow and in 'Porolepiformes' it is broad. But in *Ectosteorhachis* (an osteolepid) only the tooth-bearing part is narrow — the parasphenoid is continued forward and laterally as a broad, if thin, film of bone fused to the ventral surface of the endocranium (cf. Romer, 1937, p. 19).

3) Jarvik states that lack of the external parietal foramen is typical only of 'Porolepiformes'; both *Megalichthys* and *Ectosteorhachis* lack it, however.

Kulczycki further criticizes Jarvik's description of the snout anatomy of *Porolepis*, especially the detailed description of the nasal capsule and the canals for nerves and vessels (see especially Kulczycki, 1960, pp. 81-94). On the other hand, Jarvik states (in press) that in most details the new material he has of *Glyptolepis* fully bears out his description of *Porolepis*.

DISCUSSION AND CONCLUSIONS

The nature of the fossil remains, by which the Rhipidistia are known, is extremely variable, ranging from the excellent and fairly plentiful material preserved 'in the round' of *Eusthenopteron*, *Ectosteorhachis* and *Glyptolepis* (Jarvik, in press, and in preparation), to the fragments of skulls, isolated teeth, and scales typical of most genera. It is not surprising, therefore, that most phylogenies and taxonomic studies have been based on the histology of teeth and scales. The latter approach is, of course, open to some doubts and reservations, but the recent work of Ørvig seems particularly important (see Ørvig, 1957, p. 409 for phylogeny).

It is especially interesting to note the positions assigned by Ørvig to *Panderichthys* and *Platycephalichthys*. According to Jarvik's interpretations of crossopterygian anatomy, the presence of the pars ethmoidalis cranialis in both genera and the two external nares in *Panderichthys* would ally them with the *Porolepis lineage*. All other evidence, however (Ørvig and Vorobjeva), opposes this view and maintains their 'osteolepiform' status. One is forced to conclude that these two characters are more labile than was formerly supposed; they fail to show correlation with other, diagnostic, characters.

Schmalhausen (1959) rejected Jarvik's theories on the grounds that the two 'types' of skull merely reflected the relative proportions of the skull, *Porolepis* being broad-snouted and *Eusthenopteron* narrow-snouted. Schmalhausen was referring particularly to the difference between the two types of anterior

palatal fenestra, the nature of which we have already seen to depend on the type of lower jaw dentition. Although Schmalhausen's idea is an attractive one, it does not explain the discrepancy in the occurrence of the pars ethmoidalis cranialis. The 'Osteolepiformes' contain both broad and narrow snouted forms, but the presence of the pars ethmoidalis cranialis is independent of this factor:

		Snout	Pars ethmoidalis cranialis
Osteolepidae	*Ectosteorhachis*	Broad	Absent
	Panderichthys	Narrow	Present
Rhizodontidae	*Eusthenopteron*	Narrow	Absent
	Platycephalichthys	Broad	Present

This character is not even related to the relative width of the internasal wall, which seems to be dependent on the relative size of the nasal capsules rather than on the external proportions or intrinsic 'osteolepiform'/'porolepiform' nature of the snout.

I can think of no explanation of the apparently random occurrence of these characters except that the Rhipidistia form a fairly close-knit group within which comparable variations can occur in all families.

There is no doubt that a distinction of some sort can be drawn between a porolepiform and an osteolepiform assemblage (although the former is a much more compact group than the latter). The controversy lies in the status to be assigned to each. The two groups have been interpreted by Jarvik (1942, 1955, 1960) to represent a fundamental split within the Rhipidistia and, by extrapolation, within the recent Amphibia also. There are two major objections to the arguments which are presented to substantiate this hypothesis. Firstly, only one genus of 'Osteolepiformes' (*Eusthenopteron*) was available for consideration in any detail, and secondly, all the characters dividing the two groups are chosen with reference to the proposed relation to the Urodela or Anura and not at all with reference to the Rhipidistia in general. Taking into consideration the evidence presented above and bearing in mind other more detailed points such as are disputed by Kulczycki and to which I hope to return in a future work, it seems that the two groups of Rhipidistia are more closely related than has been stated. Furthermore, those characters which might reflect a relationship with particular

recent Amphibia are present in both groups of rhipidistians and are not, therefore, justifiably so considered.

From my own studies of the Rhipidistia, I personally favour the view propounded by Berg (1958) that there are three groups of Rhipidistia: the Porolepiformes, the Osteolepiformes and the Rhizodontiformes. I would allow each group no more than super-familial rank.

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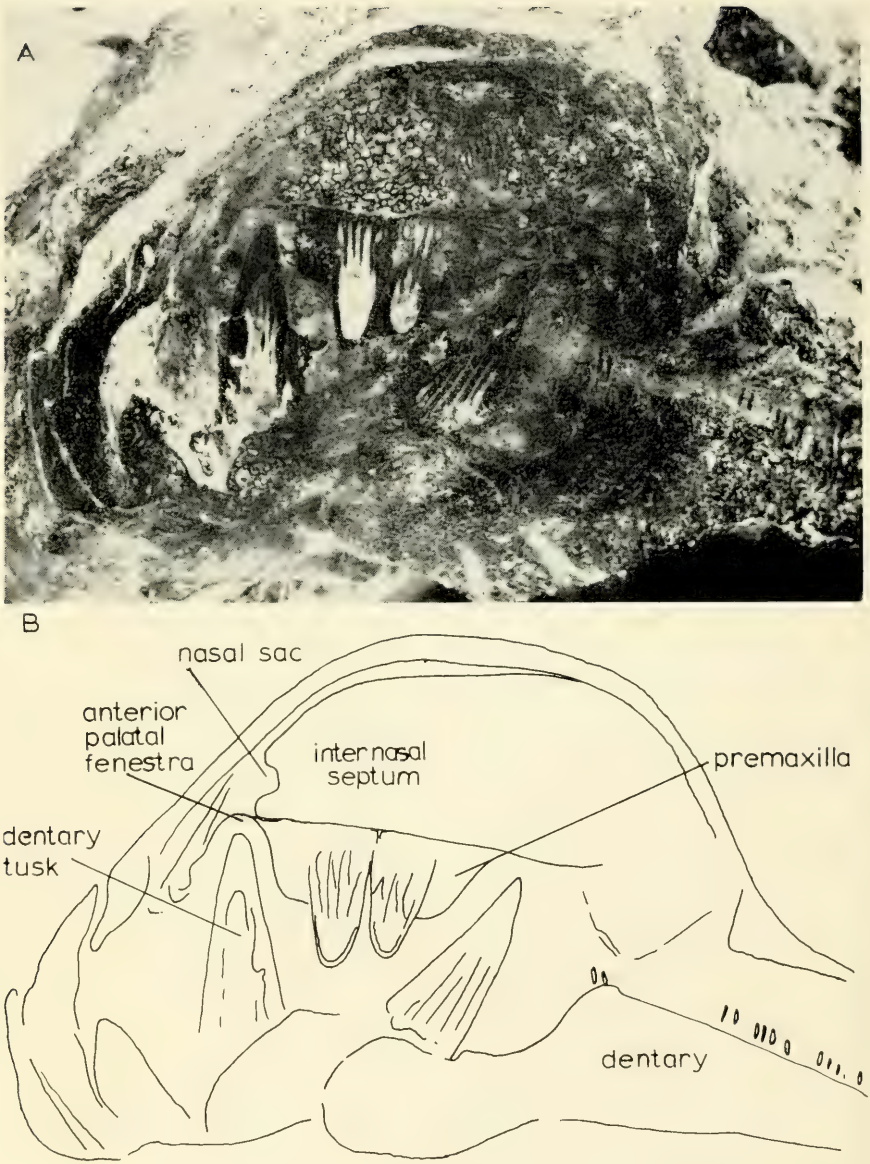

Plate 1.

Megalichthys from the Scottish Carboniferous. M.C.Z. 8941. Tip of the snout in anterior view, showing premaxillary teeth, dentary tusks, and the anterior palatal fenestrae exposed by a natural break in the specimen:

A. Photographed immersed in water.

B. Semi-diagrammatic sketch of A, emphasizing the pertinent features.

BREVIORA

Museum of Comparative Zoology

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ON A NEW SPECIES OF THE EARTHWORM GENUS *TRIGASTER* BENHAM 1886 (OCTOCHAETIDAE)[1]

By G. E. GATES

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The presence, in Cuba, of an apparently endemic *Trigaster* is of such zoogeographical importance as to contra-indicate further and perhaps indefinite delay in publishing available data.

TRIGASTER CAVERNICOLA n. sp.

"Cueva de Colón," Punta Caguanes, Yaguajay, Las Villas Province, Cuba, 0-0-1. G. S. Taboada. (Type in the Museum of Comparative Zoology.)

External characteristics. Size, 143 by 5 mm. Segments, 276. Prostomium, epilobous, tongue open posteriorly but crossed by a deep transverse furrow near anterior margin of i. Setae, $AB < CD < AA$ which is ca. = or slightly $< BC$, DD ca. = ½C. First dorsal pore, at 8/9.

Clitellum, faintly indicated, possibly saddle-shaped and reaching down only to *A*, on (xiii?)xiv-xix(xx?). Spermathecal pores, minute, superficial, midway between *A* and *B*, two pairs, equatorial in viii-ix. Female pore, at *A* and midway between 13/14 and eq/xiv, on left side. Male and prostatic pores, as well as apertures of setal follicles in the male area, unrecognizable. Seminal grooves, deep and wide, about at *B*, between eq/xvii and xix/eq. Genital markings, unpaired, transversely placed, in *AA*, each with a deep transverse, central groove, primarily postsetal on xvi, primarily presetal on xx and xxi but perhaps crossing sites of 19/20 and 20/21.

Internal anatomy. Septa, 6/7-10/11 muscular and opaque, 11/12 membranous but with discrete muscular strands. Pigment,

[1] From research financed by the National Science Foundation.

red, recognizable only in region of mD, in or associated with the circular musculature.

Gizzards, large, in v and vi. Esophagus, deeply constricted at insertions of 11/12-13/14, in xi-xiii with a bifid ventral typhlosole and numerous low, rounded, irregular ridges that are gorged with blood, without discrete calciferous glands. Intestinal origin, apparently in xv. Caeca, intestinal typhlosoles and supra-intestinal glands, lacking.

Dorsal blood vessel, single, complete, bifurcating under the brain, the branches uniting over subpharyngeal ganglion to become the ventral trunk. Extra-esophageal trunks, blood filled and recognizable alongside the ventral trunk in three segments, posterior portions empty and invisible. Supra-esophageal trunk, recognizable only in x-xiii. Subneural trunk, presumably lacking as no trace of one was found. Hearts, of x-xii are apparently lateral as no bifurcations to supra-esophageal trunk were seen, hearts of xiii latero-esophageal.

Nephridia, in at least six longitudinal ranks posteriorly, those of the median rank on each side larger than the others (or median rank composite?).

Male funnels, rather small and thick, without folds, in x-xi. Seminal vesicles, finely acinous, soft, in xii, none recognizable in coagulum of xi. Prostates, 3-4 mm. long, an ectal portion about one half mm. long and with a muscular sheen presumably being the duct. Penial and copulatory setae, not found. GM glands, apparently lacking.

Spermathecae, fairly large, adherent to posterior faces of septa and to parietes. Diverticulum, nearly spheroidal, sessile on the duct just below the ampulla. Ovaries, fan-shaped, each with several quite long egg strings.

Reproduction. Spermatozoal iridescence is lacking in the opaque coagulum of spermathecal diverticula and probably also on the male funnels. Ovaries are fully mature but the clitellar epidermis is only slightly tumescent. Postsexual regression may have been under way and if so biparental reproduction is, perhaps, to be anticipated.

Ingesta. Soil, brownish.

Remarks. The type was received in May 1958 for identification. Better material, fully clitellate if possible, was requested from the collector. Directions for preservation were not followed and subsequent specimens from the type site (received in August, 1958) were not identifiable as to genus or family. A search in

the cave during the dry season of "Freedom Year" (1959) by the same person was fruitless. Collecting in the immediate vicinity of Cueva de Colón at the appropriate season was then recommended as the species is unlikely to be confined to caves. Unfortunately, receipt of further collections in the near future now seems to be as unlikely as during the past three years.

Though the characterization above leaves much to be desired the species is distinguishable from its congeners by location of the spermathecal pores.

Key to species of *Trigaster*

1. Gizzards, two 2
   Gizzards, three 3
2. Spermathecal pores at (or slightly behind?) intersegmental furrows, spermathecae adiverticulate ..... *tolteca* (1)
   Spermathecal pores equatorial, spermathecae diverticulate ..... *cavernicola*
3. Pigmentation, dense, red, resistant to alcohol and formalin ... *rufa* (2)
   Pigment, lacking or not as in *rufa* 4
4. Spermathecae adiverticulate and with pores in *AB*, gizzards in vii-ix ..... *lankesteri* (3)
   Spermathecae diverticulate and with pores at (unpaired?) or close to mV, gizzards in v-vii ..... *intermedia* (4)

(1) *T. tolteca* Eisen, 1900, Proc. California Acad. Sci., (3) 2, p. 203. Known only from the original description of a single specimen from Toluca, Mexico, at 8000 feet. Type (lost in San Francisco earthquake?), abnormal, preservation "indifferent." Testes are said to be present in x.

(2) *T. rufa* nom. nov. for *Trigaster* sp. Gates, 1954, Bull. Mus. Comp. Zool., Harvard College, 111, p. 244. Known only from the very meager description of two macerated specimens from Luquillo Forest, at 1800 feet, Porto Rico.

(3) *T. lankesteri* Benham, 1886, Quart. Jour. Micros. Sci., 27, p. 94. Known only from the original description of the anterior portion of a single specimen from St. Thomas, West Indies. Whereabouts of the type, if still extant, is unknown. Errors in text as well as figures and/or abnormality are suspected. Testes, male funnels and seminal vesicles were not found (lost from sections?) but the amputee was clitellate and the record of spermathecal sperm (the only one for the genus) enables an assumption that reproduction is biparental. Michaelsen assigned Benham's form the rank of typical subspecies, and named two additional subspecies.

(4) *T. lankesteri intermedia* and *calwoodi* Michaelsen, 1900, Das Tierreich, 10, p. 235. Erected on three (or more?) specimens from St. Thomas, one juvenile, one clitellate but stretched and presumably macerated, and one that may have been aclitellate and not quite so much stretched. Types, if extant, presumably in the Hamburg Museum but information as to their fate and condition as yet unavailable. Such information about the two taxa

as was vouchsafed by Michaelsen is in the definitions of his Tierreich monograph. Differences between *intermedia* and *calwoodi* now seem unimportant but specific distinction from *lankesteri* does seem possible if Benham's characterizations of gizzards, spermathecae, clitellum, etc., are correct.

DISCUSSION

In *Trigaster* a simple digestive system without calciferous and supra-intestinal glands, intestinal typhlosoles and caeca but with two or three esophageal gizzards is associated with a meroic excretory system possibly much like that of other octochaetid genera such as *Eutyphoeus* and *Eudichogaster*. Four prostates and four spermathecae, supposedly ancestral in the classical phylogenies, have been retained throughout but unassociated with penial and copulatory setae. Although testes were said to be present in x of one species (*cf.* notes above), absence of all seminal vesicles except those of xii suggests that each species is functionally metandric.[2]

None of the trigasters seems to be common and all may be restricted to more or less remote habitats difficult of access from routes usually travelled by man. None of the species is known to have been transported and all are believed to be endemic.

The generic range is from Mexico through Cuba[3] and Porto Rico to the American Virgins. The new Cuban species appears to to be more closely related to the Mexican one. The Porto Rican species seems to be closer to those of St. Thomas.

Earthworms (of course after exclusion of the transported forms), because of their confinement to, breeding in, and slow migration through the soil, long have been believed to be second in paleogeographical importance to no other group of animals. *Trigaster*, perhaps more than any other North American genus, now seems likely to provide especially interesting data if the native faunas of the Mexico-Virgin axis can be studied before they are too profoundly affected by human interference with their habitats.

[2] Male funnels of x, in other octochaetid genera, frequently are retained after the testes of that segment ceased to mature sperm.

[3] Little is known of the oligochaete faunas of the West Indies, including Hispaniola. Indeed, nothing at all is known of the oligochaetes of Santo Domingo.

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